

**NASA TECHNICAL
TRANSLATION**



NASA TT F-650

2.1

**LOAN COPY: RE
AFWL (DO
KIRTLAND AF**

0069204



TECH LIBRARY KAFB, NM

0

PROBLEMS OF PHYSIOLOGICAL OPTICS

**Volume 15 - Physiology of Vision
Under Normal and Extremal Conditions**

Edited by V. G. Samsonova et al.

Academy of Sciences USSR

"Nauka" Press, Leningrad Branch

Leningrad, 1969

NATIONAL AERONAUTICS AND SPACE ADMINISTRATION • WASHINGTON, D. C. • NOVEMBER 1971

NASA TT F-650



PROBLEMS OF PHYSIOLOGICAL OPTICS
Volume 15 - Physiology of Vision Under
Normal and Extremal Conditions

V. G. Samsonova, Editor-in-Chief

A. I. Bogoslovskiy, Ed.

V. D. Glezer, Ed.

V. V. Meshkov, Ed.

Ye. N. Semenovskaya, Ed.

Translation of "Problemy Fiziologicheskoy Optiki, Tom XV;
Fiziologiya zreniya normal'nykh
i ekstremal'nykh usloviyakh"

Academy of Sciences USSR, Nauka Press,
Leningrad Branch, Leningrad, 1969

NATIONAL AERONAUTICS AND SPACE ADMINISTRATION

For sale by the National Technical Information Service, Springfield, Virginia 22151

price \$3.00

TABLE OF CONTENTS

COURSE OF DEVELOPMENT OF THE PHYSIOLOGY OF VISION AND OF PHYSIOLOGICAL OPTICS IN THE USSR OVER THE LAST 50 YEARS — V. G. Samsonova	1
 I. PHYSIOLOGY OF HUMAN VISION AND SIMULATION OF THE VISUAL SYSTEM	
SIMULATION OF THE COLOR VISION PROCESS IN MAN — D. A. Shklover	6
CERTAIN PSYCHOPHYSIOLOGICAL PRINCIPLES OF COLOR PERCEPTION DESCRIBED BY A NONLINEAR MODEL — A. V. Matveyev	19
DEDUCTIVE CONSTRUCTION OF A MODEL FOR THE LOWER METRIC OF COLOR — Yu. P. Shabanov-Kushnarenko	28
OPERATOR ANALYSIS OF ELECTRORETINOGRAMS — D. S. Melkonyan and L. G. Barsegyan	32
POSSIBLE FORMS OF COLOR VISION — N. V. Lobanova	43
METHODS OF SPECTRAL INDICATION — Ye. B. Rabkin	48
LIGHT AND COLOR THRESHOLDS OF LIGHTS AGAINST A BACKGROUND OF DIFFERENT BRIGHTNESS — R. L. Fol'b and S. V. Voronina	54
COLOR DISCRIMINATION IN PERSONS WITH LOW VISUAL ACUITY — A. I. Kaplan	61
MICROINTERVAL ANALYSIS OF THE DEVELOPMENT OF VISUAL PERCEPTION — P. O. Makarov	65
INVESTIGATION OF THE CRITICAL DISCRETENESS INTERVAL OF THE VISUAL SYSTEM — L. P. Grigor'yeva and Ye. N. Sokolov	70
THE RETINA AS AN INDICATOR OF CORTICAL INDUCTION PHASES — P. G. Snyakin and A. P. Anisimova	80
TIME OF VISUAL PERCEPTION UNDER THE ACTION OF THERAPEUTIC X-RAY DOSES ON THE DIENCEPHALO- HYPOPHYSIAL REGION — G. I. Nemtseyev and N. S. Kharon .	85
FUNCTIONAL EFFICIENCY OF THE VISUAL ANALYSOR DURING WORK WITH MICROSCOPES — N. I. Zoz	91

II. ELECTROPHYSIOLOGY AND BIOPHYSICS OF VISION

SHORT-LATENCY PROCESSES IN THE VISUAL SYSTEM OF CATS — I. A. Shevelev	95
RECRUITING OF NEURONS OF THE RABBIT SUPERIOR COLLICULI IN RESPONSES — N. V. Dubrovinskaya	99
INFLUENCE OF PROLONGED PHOTIC AND ACOUSTIC STIMULI ON UNIT ACTIVITY IN THE LATERAL GENICULATE BODY OF RABBITS — T. G. Beteleva	105
HYPOTHALAMIC POTENTIALS EVOKED BY PHOTIC STIMULATION OF THE RETINA — A. S. Novokhatskiy	113
LIGHT-EVOKED POTENTIALS IN HEALTHY PERSONS AND IN PATIENTS WITH PATHOLOGICAL LESIONS IN VARIOUS PARTS OF THE VISUAL SYSTEM — Ye. N. Semenovskaya, A. I. Bogoslovskiy, and V. K. Zhdanov	120
PHOTOREACTIVITY OF THE PIGMENTED EPITHELIUM OF THE EYE — M. A. Ostrovskiy	131
NEW DATA ON THE MECHANISMS OF ACTION OF IONIZING RADIATION ON FUNCTIONAL PROPERTIES OF THE RETINA — G. G. Demirchoglyan	136

III. SPACE AND AVIATION PHYSIOLOGY OF VISION

BASIC PROBLEMS OF THE PHYSIOLOGY OF THE VISUAL ANALYZER UNDER EXTREMAL CONDITIONS — Yu. P. Petrov	141
EFFECT OF SPACEFLIGHT FACTORS ON VISUAL FUNCTIONS — Yu. P. Petrov	148
INVESTIGATION OF SPATIAL VISION OF A FLIGHT CREW — K. S. Petrov	153
STUDY OF ACHROMATIC AND CHROMATIC VISUAL SENSITIVITY DURING SHORT PERIODS OF WEIGHTLESSNESS — L. A. Kitayev-Smyk	155
ROLE OF CONVERGENCE IN DISTANCE PERCEPTION DURING THE LANDING OF AN AIRCRAFT — Yu. V. Kamenshchikov ..	160
STUDY OF DYNAMIC VISUAL ACUITY — M. G. Kozyr'kova	164
RESTORATION OF VISUAL ACUITY AFTER A BRIGHT LIGHT FLASH OF SHORT DURATION — V. A. Khitun, P. A. Korzun, V. I. Shostak and Ye. A. Obukhova	169
CERTAIN FEATURES OF THE EFFECT OF SHORT-TERM SUPER-BRIGHT LIGHT FLASHES AGAINST A BACKGROUND OF TOTAL DARK ADAPTATION — V. I. Shostak	172

IV. OPTICS AND HISTOCHEMISTRY OF THE EYE, RESEARCH METHODS

ON THE PROBLEM OF THE REFRACTION OF THE FISH EYE — P. B. Bogatyrev	175
HISTOCHEMICAL HETEROGENEITY OF RETINAL NEURONS EXEMPLIFIED BY DISTRIBUTION OF ACID PHOSPHATASE ACTIVITY — M. A. Ostrovskiy and S. Ye. Polyak.	186
A STUDY OF THE FUNDUS OCULI IN POLARIZED LIGHT — R. M. Tamarova	192
USE OF POLARIZED LIGHT TO STUDY THE ANATOMY, PHYSIOLOGY, AND PATHOLOGY OF THE FUNDUS OCULI — D. I. Mitkokh	200
METHODS OF INVESTIGATING THE ACCOMMODATION TIME IN MAN — A. A. Sychev	205
THE METHOD OF CONSTANT PERIODS — A. I. Ivanov	209
COMPARISON OF THE BINOCULAR FUNCTIONS DURING ISO- AND ANISOMETROPIA — Yu. Z. Rozenblyum	216

COURSE OF DEVELOPMENT OF THE PHYSIOLOGY OF VISION
AND OF PHYSIOLOGICAL OPTICS IN THE USSR
OVER THE LAST 50 YEARS *

V. G. Samsonova

Reviews the history of the science of physiology of vision
in the Soviet Union.

In pre-revolutionary Russia only a few distinguished scientists worked in the field of physiological optics: M.I. Averbakh, whose investigations into the dioptrics of the eye have not lost their significance even today; P. P. Lazarev, who established the ionic theory of excitation and applied it to the study of the physiology of the eye; and L. A. Orbeli, who studied color vision in animals.

/3 **

Soon after the October Revolution the first centers of development of physiological optics were founded. One of these was established in Leningrad in the State Optical Institute. Here in 1923 was founded a laboratory of physiological optics, where the optics of the eye, its correction, and the problem of increasing the working efficiency of the visual system were studied: this laboratory was directed by L. N. Gassovskiy. A laboratory of colorimetry and color vision was organized somewhat later. G. N. Rautian, L. I. Demkina, and their colleagues N. I. Speranskaya, Ye. N. Yustova, and N. V. Lobanova, who conducted some major research into the thresholds of color perception, curves of spectral sensitivity, and many other aspects of color vision, worked here in close scientific contact with N. D. Nyuberg. The work of M. M. Gurevich and A. A. Gershun in the laboratory of photometry began at about the same time; they studied the sensitivity of the eye to light and contrast, and the theoretical and practical aspects of illumination technology. All research in physiological objects at the State Optical Institute developed under the direction of S. O. Mayzel', who subsequently trained a group of scientists at the All-Union Electrical Engineering Institute in Moscow (S. G. Yurov, R. L. Fol'b, D. A. Shklover, V. S. Khazanov, and others). A second center was established in Moscow in P. P. Lazarev's laboratory. It was there that such well-known scientists as S. I. Vavilov, S. V. Kravkov, and N. T. and V. I. Fedorov, who subsequently developed their own fields of research and trained a new generation of scientists,

* From the Inaugural Address to the Fifth Conference on Physiological Optics held on October 27, 1966.

**Numbers in the margin indicate pagination in the foreign text.

began their work. Both Fedorovs were leading specialists in the field of color vision; later they organized an important laboratory at the All-Union Institute of Experimental Medicine where L.I. Mkrtycheva, N.N. Livshits, and other eminent researchers worked. Many of the investigations conducted in this laboratory received wide acclaim not only in the Soviet Union, but also abroad.

S. V. Kravkov's scientific interests were more varied: in conjunction with his first collaborators Ye. M. Semenovskaya and A. I. Bogoslovskiy, and subsequently with many younger scientists, he studied practically all aspects of the physiology of vision. The most important contribution made by these workers was to the study of interaction between the sense organs. Their investigations are still included in many monographs and textbooks by Russian and non-Russian writers.

/4

L. A. Orbeli returned to the study of the sense organs in the 1930's. The group of workers which he directed — A. V. Lebedinskiy, A. I. Bronshteyn, L. T. Zagorul'ko, N. V. Zimkin, A. M. Aleksanyan, A. A. Volokhov, S. M. Dionesov, and others — have conducted brilliant investigations into the mechanisms lying at the basis of interaction between neural components of the visual system. At the same time, Orbeli and his pupils began to study the physiology of vision under extremal conditions, a subject which has developed continuously since then and is doing so particularly intensively at the present time.

In those days eminent psychologists such as B. M. Teplov and A. I. Smirnov, and later, G. Kh. Kekcheyev, were engaged in the study of the physiology of vision, and they carried out interesting research into sensitivity to contrast, visual acuity, and adaptation.

In the early 1930's, P. O. Makarov, at Leningrad University, commenced his study of temporal processes in the visual system, work which is still continuing today. It was there that N. I. Pinegin made his first scientific contributions, and his work in the field of sensitivity to light and contrast is a good example of precision studies in man.

In the 1930's, a large group of lighting engineers took up the study of the physiology of vision. In Moscow V. V. Meshkov published his first-class investigations into sensitivity to contrast and blindness, distinguished by the unusual clarity, lucidity, and precision with which the problems posed were solved. The illumination engineering and hygienic aspects of the physiology of vision underwent extensive development (M. M. Dantsig, Z. M. Zolina, A. V. Roslavtsev, A. A. Trukhanov, Ya. E. Neyshtadt and others).

Meanwhile other important groups of investigators sprang up. In Khar'kov, Ye. B. Rabkin began to study anomalies of color vision, and A. I. Dashevskiy the optics of the eye. In Moscow, M. A. Vishnevskiy and B. A. Tsyrlin studied the thresholds of photic sensitivity from the standpoint of the aviation physiology of that time, while P. G. Snyakin, under N. I. Grashchenkov's direction, began his investigations into functional lability of the retina. Nor did the problem of stereoscopic vision escape the attention of Soviet physiologists (V. G. Samsonova, G. A. Litinskiy, Ye. M. Belostotskiy).

In 1934 L.N. Gassovskiy, with support from S.I. Vavilov and L.A. Orbeli, organized an All-Union Conference on Physiological Optics at the State Optical Institute which was attended by 156 delegates and 200 guests; 58 papers were read at the conference. The number of delegates and the number of papers are a clear illustration of the scale of development reached by the physiology of vision at that time in the USSR.

Several new laboratories were founded in the prewar period: at the All-Union Electrical Engineering Institute, at the Institute of Experimental Medicine, and at the Institutes of Work Safety in Moscow and Leningrad. This was an exceptionally fruitful period for scientific work, and much research of world-wide importance was carried out, which has not lost its significance even today. Many investigations were of practical importance and were used to increase the productivity of labor and in military physiology. During World War II, specialists in physiological optics made many useful contributions to the Nation's war effort.

Before the war the journal "Problemy Fiziologicheskoy Optiki" (Problems in Physiological Optics) was first published, and at the height of the war, in 1943, the Committee for Physiological Optics of the Academy of Sciences of the USSR was organized. It was headed by L.A. Orbeli, and his deputies were S.I. Vavilov and M.I. Averbakh, while the scientific secretary was S.V. Kravkov. This Committee carried out considerable administrative work in the war and postwar periods. Issues of the "Problemy" were regularly published, and every year seven or eight scientific meetings were held, at which papers were read, scientific problems were discussed, and trends in research of the greatest importance to theory and practice were examined. In 1946 an All-Union Conference was organized, demonstrating the great scientific progress made in many different fields of physiological optics. In this period extensive research was conducted into color vision, the principles governing absolute and differential thresholds, visual acuity, engineering aspects of the physiology of vision, inter-neuronal relationships between individual components of the organ of vision, interaction between the sense organs, and stereoscopic vision, and electro-physiological investigations into the human visual system were started. /5

In the early 1950's, physiological optics suffered grievous losses. During the war, M.I. Averbakh, P.I. Lazarev, and V.I. Fedorova had died. After the 1950's, S.I. Vavilov, L.A. Orbeli, S.O. Mayzel', S.V. Kravkov, A.V. Lebedinskiy, and N.T. Fedorov were no longer with us. Death carried away A.A. Aleksanyan, Ye.M. Belostotskiy, A.I. Bronshteyn, A.A. Gershun, N.I. Grashchenkov, L.T. Zagorul'ko, G.Kh. Kekcheyev, A.V. Roslavtsev, G.N. Rautian, and B.M. Teplov. The death of all these authorities in physiological optics, coupled with the extensive reorganizations and the destruction of some laboratories, and other changes meant that much of the work on the mechanisms of human vision had to be stopped or greatly curtailed. During these years great changes were also made in the directions of research, and new important fields began to be explored, notably neurophysiological and morphological, which had hitherto been poorly represented in the USSR.

At the 4th Conference on Physiological Optics in 1955, 14 papers were read on electrical responses of the visual system, whereas at the conference in 1946 there were only two.

In the next decade, research began into the mechanisms of photoreception and, in particular, into visual pigments, many new laboratories were created, especially of a neurophysiological and biophysical character, and the function of the visual system under extremal conditions was studied. In the Academy of Sciences of the USSR, laboratories for this purpose were established in the I. P. Pavlov Institute of Physiology, directed by V.D. Glezer, in the Institute of Evolutionary Biochemistry, headed by Ya. A. Vinnikov, in the Institute for Problems of Information Transmission, headed by M.M. Bongardt, in the Institute of Higher Nervous Activity and Neurophysiology, headed by V. G. Samsonova, in the Institute of Morphology of Animals, headed by G. D. Smirnov, in the Institute of Automation and Telemechanics, headed by N. V. Pozin, in the Institute of Physiology of the Academy of Sciences of the Armenian SSR, headed by G. G. Demirchoglyan, and also in many other research institutes and higher educational establishments in the USSR, such as Moscow University (director, Ye.N. Sokolov), and so on. Fruitful work has also continued at long established laboratories at the State Optical Institute, at Leningrad University, at the Helmholtz Institute of Ophthalmology (A.I. Bogoslovskiy and Ye.N. Semenovskaya), at the Institute of Physiology, Academy of Medical Sciences of the USSR, at the All-Union Institute of Illumination Engineering, at institutes of work safety, and at many other establishments.

/6

More recently, tremendous changes have taken place in the methods used to study the organ of vision, and new and very promising approaches have been developed, such as the analytical, in which the mechanisms of activity of the visual system are investigated not only at the cellular, but also at the subcellular levels; step by step, from responses of single cells and from their combined responses, from biochemical and biophysiological indices, the complexity of mechanisms of stimulus transformation at all levels of the visual system is being elucidated and mathematical and logical models, for subsequent application to engineering, are being created.

Nowadays annual symposia are held on individual problems in the physiology of vision, and in October, 1966, the 5th Conference on Physiological Optics was held in Moscow, at which the following scientist read papers.

On morphology of the organ of vision: 1) Ya. A. Vinnikov, 2) A. S. Novokhatskiy, 3) N. G. Fel'dman.

On electrophysiology of the visual system: 1) V. V. Baranovskiy and V. G. Lysenko, 2) A. V. Bertulis and N. B. Kostelyanets, 3) T. G. Beteleva, 4) A. L. Byzov, 5) V. B. Val'tsev, 6) Ye. Ya. Voytinskiy, R. Ya. Yermolayeva, and K. N. Kharauzov, 7) V. D. Glezer, Yu. G. Troshikhina, and I. I. Dashin, 8) G. G. Demirchoglyan, 9) N. V. Dubrovinskaya, 10) T. M. Zagorul'ko, N. P. Veselkin, and M. G. Belekova, 11) G. M. Zenkin, 12) V. A. Ivanov, 13) O. Yu. Orlov, 14) M. A. Ostrovskiy, 15) V. B. Polyanskiy, 16) Ye. N. Semenovskaya, A. I. Bogoslovskiy, and V. K. Zhdanov, 17) I. A. Shevelev and V. M. Krol'.

On simulation of the visual system and visual identification of form: 1) V.D. Glezer and A.A. Nevskaya, 2) A.B. Matyeyev, 3) D.S. Melkoyan and L.G. Barsegyan, 4) N.V. Prazdnikova, 5) M.A. Fayermark, 6) D.A. Shklover.

On color vision: 1) A.I. Kaplan, 2) P.A. Korzun, 3) N.V. Lobanova, 4) G.A. Mazokhin and T.M. Vishnevskaya, 5) N.D. Nyuberg, 6) Ye.B. Rabkin, 7) R.A. Fol'b and S.V. Voronina, 8) V.S. Khazanov.

On the physiology of vision under extremal conditions: 1) A.N. Zolotukhin, 2) Yu.V. Kamenshchikov, 3) N.G. Kozyr'kova, 4) L.A. Kitayev-Smyk, 5) E.S. Kotova, 6) N.G. Medvedeva, 7) B.M. Savin, 8) T.A. Petrova, M.P. Kuz'minykh, I.Ya. Yakovleva, and V.P. Baranov, 9) Yu.P. Petrov, 10) I.S. Petrov, 11) V.I. Shostak.

On binocular and stereoscopic vision: 1) N.I. Gol'tsman, 2) Ye.I. Ivanova, 3) T.P. Kashchenko, 4) L.I. Leushina, 5) R.N. Lur'ye and I.L. Smol'yaninova, 6) A.I. Kogan, 7) V.P. Neverov, 8) N.A. Ovsyannikova and N.Ye. Krysenko, 9) Yu.Z. Rozenblyum, 10) N.Yu. Vergiles, G.V. Rodionov, L.P. Sedakova, and L.P. Shchedrovitskiy.

On hygiene of vision: 1) V.I. Beletskaya, 2) I.L. Zarenina, 3) N.I. Zoz, 4) Z.M. Zolina, 5) N.V. Shubina, 6) Ye.M. Orlova.

On pathology of the visual system: 1) A.S. Buyko, 2) N.S. Yeremina, 3) R.Ya. Yermolayeva, 4) R.B. Zaretskaya, 5) G.I. Nemtseyev, N.S. Kharon, 6) G.V. Panfilova, 7) Ye.N. Sokolov and L.P. Grigor'yeva.

On other aspects of the psychophysiology of vision: 1) M.S. Smirnov, 2) A.L. Yarbus.

On new methods of investigation of the visual system: 1) A.D. Vladimirov, 2) A.I. Ivanov, 3) S.K. Lisitsyn and G.I. Nemtseyev, 4) A.V. Roslavl'tsev and N.A. Koval'chuk, 5) A.A. Sychev, 6) R.M. Tamarova and D.I. Mitkokh, 7) L.S. Urmakher.

/7

It will be clear from this list that the electrophysiology of the visual system, aspects of its simulation, the physiology of vision under extremal conditions, and problems concerned with color vision and stereoscopic vision constitute the principal topics for research in physiological optics in the Soviet Union at the present time.

Only those papers read at the conference which have never been published before are included in this collection.

I. PHYSIOLOGY OF HUMAN VISION AND SIMULATION OF THE VISUAL SYSTEM

SIMULATION OF THE COLOR VISION PROCESS IN MAN

D.A. Shklover

Description of a mathematical model for the human color vision process where the output signals correspond to experimental functions obtained under specific observational conditions. The model is used to explain several characteristic features of the color vision system in man. An electronic analog is outlined which reproduces the main functions of the system and which can be used to develop photoelectric methods of color measurement. The electronic analog is applied to problems involving the color resolution of the eye under different circumstances.

1. The object of simulation of the color identification process is to establish mathematical relationships between the spectral composition of the radiation and the color sensations determined by its color tone, its color saturation, and its luminosity. /8

Color sensations from a given point of an observed field are not in general determined absolutely by the spectral composition of the emitted light. Because of color adaptation, visual induction, eye movements, and so on, color sensations depend on the distribution of spectral brightnesses over the whole field of vision, both at the moment of observation and in the preceding period. To begin with, let us examine the color vision process in the simplest case, that of observation of a field of uniform color, subtending an angle of $2-10^\circ$ at the eye and with a luminance of $10-1000$ nits, against an absolutely black background for an unlimited period of time. Under these fixed conditions, the spectral distribution of the luminous energy of the observed field in the visible part of the spectrum can be taken as the input signals entirely determining the color sensations. In turn, the spectral luminance (B_λ) is determined by the spectral intensity of illumination (E_λ) created on the observed surface by a luminous source and the spectral coefficient of luminance of the surface (p_λ):

$$B_\lambda = E_\lambda p_\lambda. \quad (1)$$

It is important to note that the human eye must be able to distinguish the color of objects despite considerable changes in their luminance (10^3 — 10^4 times), and also from their spectral composition.

2. It is now regarded as firmly established that the principle of spectral resolution is not used in the human visual system. The work of the color-discriminating system in man and animals is based on the use of radiation receivers of integral type, with selective curves of spectral sensitivity. By radiation receiver is meant any biological, physical or chemical device capable of responding to radiant energy irrespective of the character of the response (a change in chemical structure, a pulse of electric current, and so on). Let us examine to begin with radiation receivers with linear additive responses. In this case, the response of the receiver U_i to radiation of given spectral composition is determined (1, 2) by the value of the definite integral:

$$u_i = \int_{\lambda_1}^{\lambda_2} B_{\lambda} \varphi_{\lambda} d\lambda,$$

where B_{λ} represents the spectral intensity of emission; φ_{λ} the spectral sensitivity of the receiver; and $\lambda_1 \lambda_2$ the limits of the visible spectrum. /9

It is evident that the color-discriminating power of a system of such receivers will depend on the number of receivers, on their curves of spectral sensitivity, and on the threshold level of sensitivity. The Young-Helmholtz hypothesis concerning the presence of preselective radiation receivers in the retina of the human eye has only recently (after 150 years) received direct experimental confirmation in the work of Wald [14, 25].

The problem of the number of photosensitive receivers in the eye can also be unequivocally solved on the basis of data concerning the number of colors distinguishable by the human eye. By analogy with purely brightness sensations, assuming that the number of gradations which can be differentiated by each receiver is approximately 300, the maximum possible number of distinguishable colors and the quantity of color information of systems with different numbers of receivers can be calculated.

TABLE 1

Number of receivers	1	2	3	4	n
Number of distinguishable colors	300 ($0.3 \cdot 10^3$)	300^2 ($90 \cdot 10^3$)	300^3 ($27 \cdot 10^6$)	300^4 ($8.1 \cdot 10^9$)	300^n
Quantity of information, bits	8.2	16.4	24.6	32.8	$8.2 \cdot n$

In fact, the human eye can distinguish about 10 million colors. Considering that the number of actually possible combinations of responses of the receivers is limited by the volume of the colored body (see below), this number shows good agreement with the maximum number for a system of three receivers calculated theoretically. It must be remembered that an increase in the number of receivers from 3 to 4, with no change in their size, can lead not only to a considerable excess of color information, but also to a decrease in visual acuity.

Processing of visual information in the primary receivers of the retina thus reduces the excess of information due to variations in the spectra of reflection of the observed objects. A wide variety of possible colors can be represented at points in a three-dimensional color space, a subspace of an n -dimensional space of spectral functions of radiation. Responses of radiation receivers can be regarded as coordinates of the color of the radiation.

Many different spectral compositions of radiation, forming what are known as metameric radiations, indistinguishable by the eye, correspond to the same color of radiation. As Nyuberg [3] showed, the practical decrease in information as a result of its processing by the primary receivers is small, since the metameric curves are usually very similar in spectrum and have no less than three points of intersection within the limits of the visible spectrum.

3. Let us examine the question of optimal curves of spectral sensitivity of the receivers of the color-discriminating system. It is evident that narrow-band curves of spectral sensitivity would have the result that not all emissions in the visible part of the spectrum would be received by the system, and that the color space for a considerable group of emissions would be one-dimensional or two-dimensional. From this point of view, the best criteria must be the intersecting spectral curves covering considerable areas of the visible spectrum, differing in the position of their maxima of sensitivity.

Spectral sensitivity curves of the receivers of the eye can be determined by three main methods: on the basis of curves of summation of colors using data concerning vision of dichromats [4], by measuring spectral absorption curves of single retinal cones [14], and by measuring spectral sensitivity curves of the eye during strong color adaptation [25]. The results obtained by these three methods agree reasonably well (Fig. 1), but the results of Nyuberg and Yustova [4], obtained by averaging data concerning the color vision of a large group of observers, must be regarded as the most reliable for a field of vision of 2° .

/10

The region of possible colors is bounded in color space by a cone (Fig. 2), on the surface of which the color of monochromatic and purple radiations is located. The intersection of this cone with a single plane forms the chromaticity diagram of the radiation. The geometric locus of the points of radiation differing only in intensity (equal in chromaticity) consists of straight lines passing through the origin of the coordinates. For self-luminous objects, the maximum values of the color coordinates are limited only by the possible magnitudes of their intensity of emission. By examining the region of possible colors of reflecting or transparent models under assigned conditions of illumination, it can be shown [1] that the limiting values of the color coordinates for a radiation of

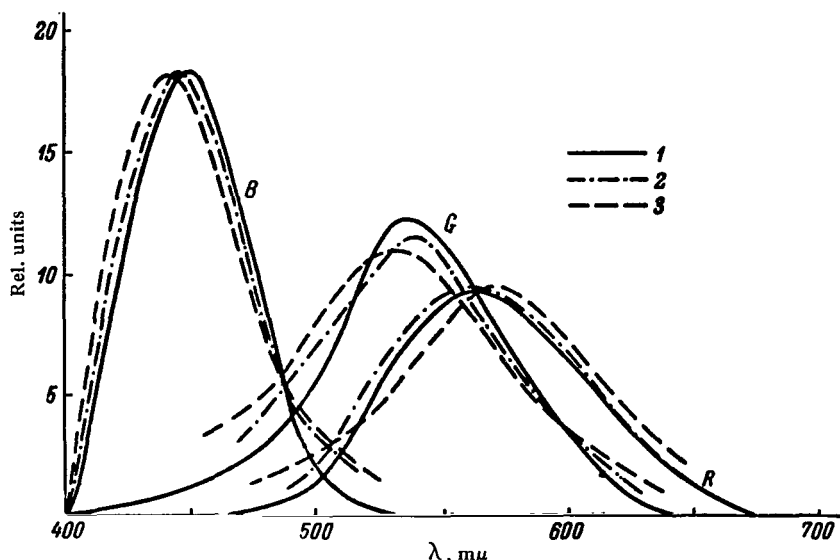


Figure 1. Spectral Sensitivity Curves of Receivers of the Human Eye. Abscissa, Wavelength of Monochromatic Light, $m\mu$; Ordinate, Sensitivity in Relative Units.
1 - Data of Nyuberg and Yustova [4], 2 - Data of Wald [25],
3 - Data of Brown and Wald [14].

any chromaticity will be less than the corresponding values of the color coordinates of an ideally white object. Under these circumstances, the maximum value of the coordinates decreases with an increase in saturation of the radiation. The real volume of color information is thus determined by the number of threshold elements within the field of color range. It is several times smaller than the limiting volume of information calculated by the writers previously for three radiation receivers. The volume of the color field depends on the spectral sensitivity curves of the radiation receivers. All other conditions being the same, the greater the volume of the color field, the greater the amount of color information. It can be shown that from this point of view the spectral sensitivity curves of the receivers of the human eye are not optimal, since the maxima of the curves R and G are very close together. Better color-discriminating sensitivity can be obtained, for example, by the use of a red-sensitive receiver with a maximum of

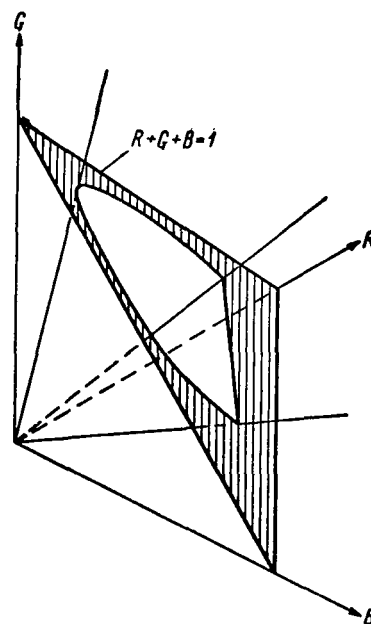


Figure 2. The Color Space RGB.

sensitivity shifted toward the long-wave part of the spectrum ($\lambda_{\max} = 600 \text{ m}\mu$), as the writers have proposed for photoelectric colorimetry [9]. It is interesting to note that radiation receivers with that type of curve are found in the retina of some animals.

The model simulating the work of primary additive receivers of the eye with linear characteristics, described above, agrees completely with the fundamental laws of addition of colors first established by Grassman on the basis of Maxwell's experiments. However, although such a system can give the right answer to questions pertaining to the monochromaticity of radiations and the laws of addition of colors, it cannot give information concerning color sensations produced by radiation of a given color or concerning the degree of discrimination (color contrast) between colors.

4. Color sensations are the product of our consciousness, and neither physiology or psychology has yet produced methods of direct quantitative estimation of sensation. The only method of estimating color sensations at present available is that of measuring the coordinates of a color corresponding to constancy or an equal degree of change of color sensations. Fundamental experimental investigations of human color vision by psychophysical methods may be as follows:

- 1) Determination of groups of radiations of different spectral composition which are completely identical as regards visual perception (monochromatic);
- 2) Determination of the color coordinates of radiations which are identical in any one characteristic of color sensation: color hue, saturation, or luminosity;
- 3) Determination of the color coordinates of radiations which differ equally in sensation from each other (in the special case, which differ by one threshold).

For reasons given above, the results of these measurements naturally depend on the conditions of observation. The experiments of the first type, reflecting the work of primary receivers of the eye only, are least critical to changes in the conditions of observation and are most accurate (zero orientations). The more the radiations to be compared differ in color, the less accurate the experiments of the second and third types. Fairly reliable results in these cases can only be obtained by statistical analysis of many measurements and by the use of the method of small steps.

/12

The experiments mentioned above can define any radiation in the form of a point in color space and can enable a family of surfaces to be plotted in it to correspond to constant and uniformly changing values of color hue, color saturation, and luminosity, averaged for a large number of observers. Having determined the equations of such surfaces as functions of color coordinates, a mathematical relationship can be established between the color coordinates (input signals) and color sensations (output signals). However, because of the decisive importance of conditions of observation, which usually cannot be strictly fixed, the low accuracy of the measurements, and the considerable

scatter between results obtained by individual observers, it is not yet possible to obtain sufficiently reliable data by this method.

It must also be pointed out that determination of the connection between the output and input signals by the "black box" method does not prove convincingly that the solution found is the only one, or that the concrete mechanism of information processing by different functional structures of the retina can be described. I therefore consider that at the present time, when constructing a model to simulate color identification, it is essential to start from definite hypotheses concerning the character of information processing by individual elements of the retina, based on the results of histological and electrophysiological experiments, and to test them by comparing the results of calculation with the results of psychophysical experiments.

5. The simplest model of primary analysis of color information described above was based on the use of receivers with linear responses. However, the results of electrophysiological [17] and psychophysical experiments show clearly that the responses of the retinal receivers are approximately logarithmic functions of the intensity of radiation (the Weber—Fechner law). The biological importance of this logarithmic relationship is that this is the only way of ensuring that the difference between sensations from particular objects remains the same during a change of several orders of magnitude in the input signals (intensity of illumination E) of the system:

$$\log E_1 \rho_1 - \log E_1 \rho_2 = \log \frac{\rho_1}{\rho_2} = \text{const.}$$

The first attempt to construct an equal-contrast color space in logarithmic coordinates was made by Helmholtz, and work in this direction was subsequently continued by Sinden [23] and Stails [24].

In 1954, the writer [10] proposed a model to simulate the formation of sensations of color hue, saturation, and luminosity (Fig. 3), based on the use of three radiation receivers with nonlinear characteristics and subsequent processing of information in a manner close to the ideas of Hering [18] and Adams [13]. This model was based on the hypothesis of the formation of luminosity signals (V_α and V_β) by paired subtraction of the responses of the three receivers (R, G, B) with logarithmic characteristics:

$$\begin{aligned} V_\alpha &= a \log (R + C) - a \log (G + C) = a \log \frac{R + C}{G + C}, \\ V_\beta &= a \log (B + C) - a \log (G + C) = a \log \frac{B + C}{G + C}, \end{aligned}$$

where C is a constant coefficient. Saturation of the light (H) in this system was defined as the root mean square of the luminosity signals, and the color hue λ was defined as the ratio between them

/13

$$H^2 = V_\alpha^2 + V_\beta^2$$

$$\tan \lambda = \frac{V_\beta}{V_\alpha}$$

It was shown that lines of constant values of saturation and color hue on the color graph V_α and V_β correspond to those found experimentally, and the color graph itself is close to equal-contrast in character. This model was analyzed in a number of subsequent papers by Soviet [11] and Western investigators [16, 19, 21]. New instruments for color measurement were suggested on its basis [7, 12], and methods of measurement of whiteness [9] and of shade differences between materials were developed.

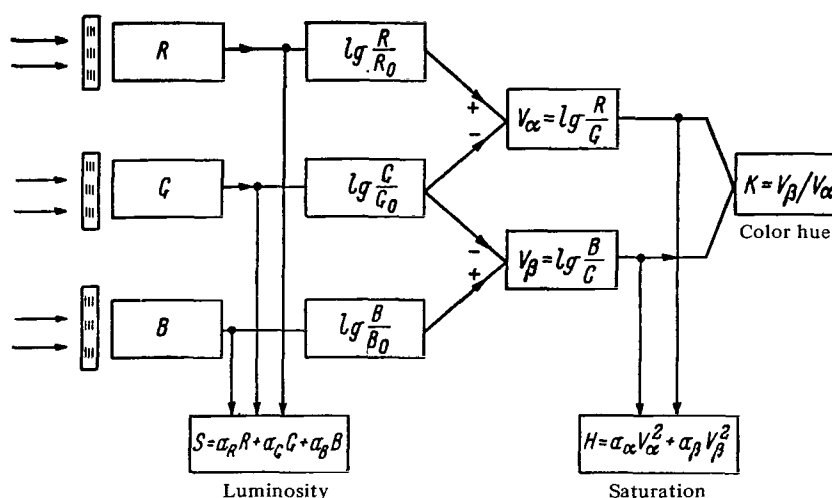


Figure 3. Scheme of Formation of Color Sensations After Shklover [10].

6. In recent years the mechanism of formation of color signals by paired subtraction of primary nonlinear signals, with the formation of signals of differing polarity, on which the model was based, has been confirmed by the work of MacNichol [20], Orlov and Maksimova [6] and others. At the same time, new research, connected in particular with the study of the relationship between perception of luminosity and brightness, and also attempts to improve agreement between the results obtained with the model and those of psychophysical experiments, made improvements in the model desirable. The new model (Fig. 4) differs from the 1954 model in having feedback units (pupil and adaptation), by the formation of three difference signals instead of two, and by a slight change in the ratios describing the sensations of color hue and luminosity.

As the work of Stevens [22] has shown, the response of the eye to achromatic radiation — the luminosity (S) — under constant conditions of preliminary adaptation is a power function of the brightness (B) of the observed radiation;

$$S = k(B - B_0)^n$$

where B_0 represents the threshold brightness and k and n are coefficients depending on the level of adaptation.

With a simultaneous change in brightness of the observed object and in the level of adaptation, the relationship between luminosity and brightness differs from the power function because of changes in the values of k and n , and if re-adaptation to the observed brightness is complete, it approximates to a logarithmic function (Fig. 5). A decrease in the sensitivity of the receiver with an increase in the brightness of adaptation is achieved in the model by using a negative feedback, changing the values of the coefficients k and n . By selecting the values of the time constants of the feedback circuits, it is possible to obtain a relationship between the response of the receivers and the intensity of the radiation under different conditions of observation which is close to that observed experimentally.

/14

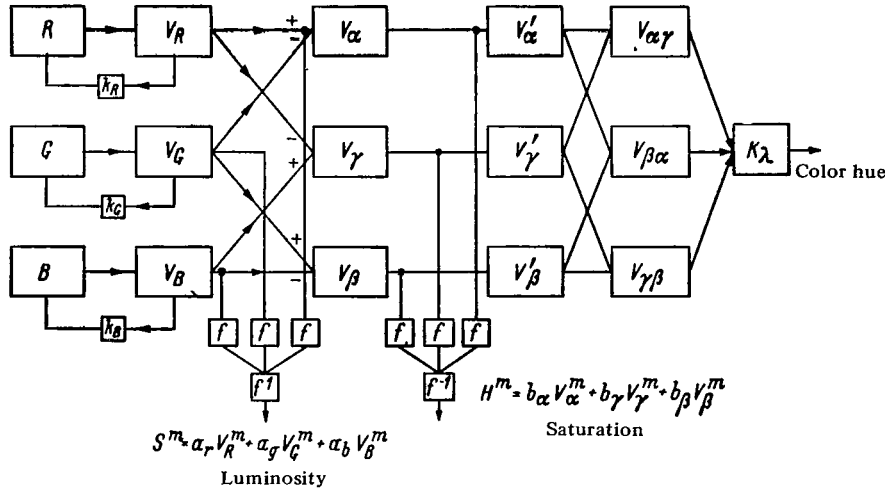


Figure 4. Model Simulating Color Vision.

Subsequent processing of the color information has the object of obtaining signals facilitating identification of the observed objects and independent of the absolute level of intensity of illumination (signals of chromaticity), and also independent of the degree of dilution of the radiation with white (signals of color hue). As was mentioned above, signals of chromaticity are formed by paired subtraction of nonlinear signals of the receivers V_R , V_G and V_B . Since recordings of difference signals from glial cells have so far been made only for certain fishes [19] and monkeys, no precise data are available on the mechanism of production of such signals in the human retina. It is therefore expedient to suggest that unequally probable participation of all receivers of radiation be assumed in the formation of these signals and, consequently, that three difference signals are formed:

$$V_{\alpha} = V_R - V_G \cong \log \frac{R}{G},$$

$$V_{\beta} = V_G - V_B \cong \log \frac{G}{B},$$

$$V_{\gamma} = V_B - V_R \cong \log \frac{B}{R}.$$

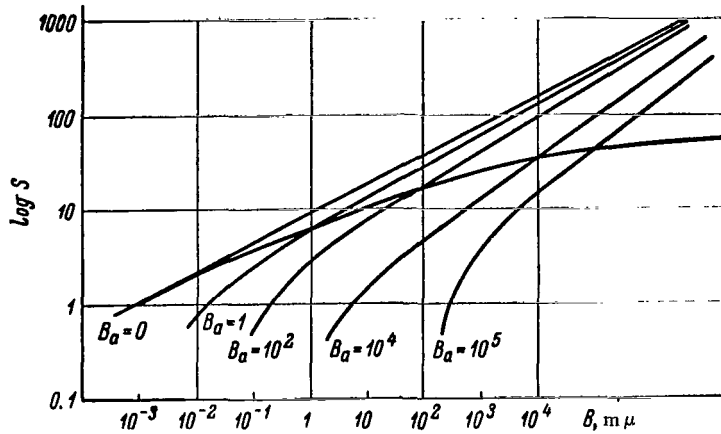


Figure 5. Luminosity S as a Function of Brightness B for Different Levels of Preliminary Adaptation B_{α} , after Stevens [22].

The magnitudes of difference signals for receivers of the human eye for monochromatic radiations of equal power but of different wavelengths are given in Fig. 6. It must be remembered that the laws of additivity are applicable only to the primary receivers of the eye, and these curves cannot therefore be regarded as curves of sensitivity of certain receivers. Since chromaticity of a radiation is a two-dimensional value, the three difference signals characterize it excessively. It is easy to show that these signals are independent, and are connected by the equation

/15

$$V_{\alpha} + V_{\beta} + V_{\gamma} = 0$$

In accordance with experimental results [25], besides the C-cells giving chromaticity signals in the retina, there are also L-cells, in which the signals of the primary receivers are summated to form the luminosity signal:

$$S = a_R V_R + a_G V_G + a_B V_B.$$

The color space in coordinates V_{α} , V_{β} , V_{γ} and S is illustrated in Fig. 7. The axes of coordinates V_{α} , V_{β} and V_{γ} must lie in the plane of constant brightness at angles of 120° to each other, while the lines of constant chromaticity consist of a bundle of straight lines parallel to the achromatic axis. The

/16

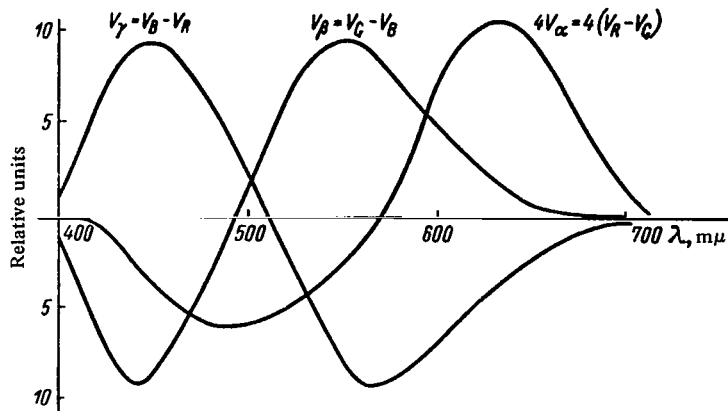


Figure 6. Relationship Between Chromaticity Signals, in Relative Units, and Wavelength for Monochromatic Radiations of Equal Power ($\gamma \text{ m}\mu$).

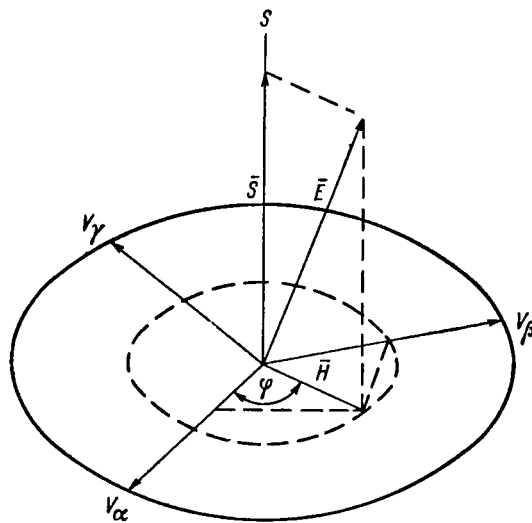


Figure 7. Equal-Contrast Color Space.
Explanation in Text.

arbitrary vector of color \bar{E} can be resolved into two components: the luminosity vector \bar{S} and the chromaticity vector \bar{H} , lying in the plane of constant brightness. The moduli of these vectors are equal to the luminosity and saturation respectively of the particular color concerned. Saturation is related to the magnitudes of the chromaticity signals by the equation:

$$H^2 = a_\alpha V_\alpha^2 + a_\beta V_\beta^2 + a_\gamma V_\gamma^2.$$

color contrast between radiations of different colors is determined by the equations:

$$\begin{aligned}\Delta L^2 &= \Delta H^2 + \Delta S^2 \\ \Delta L^2 &= \sqrt{a_\alpha \Delta V_\alpha^2 + a_\beta \Delta V_\beta^2 + a_\gamma \Delta V_\gamma^2} + \Delta S^2.\end{aligned}$$

all radiations of constant color hue lie in the color space in half-plane passing through the achromatic axis. The value of the color hue is characterized by the magnitude of the angle ϕ formed by these planes with a certain initial plane. This angle is determined absolutely by the magnitudes of the ratios between the difference signals:

$$V_{\alpha\beta} = \frac{V_\alpha}{V_\beta}; \quad V_{\beta\gamma} = \frac{V_\beta}{V_\gamma}; \quad V_{\gamma\alpha} = \frac{V_\gamma}{V_\alpha}.$$

During construction of the model an attempt was made to include only those transformations of signals which are in fact found during electrophysiological investigations of the retina. Such transformations include nonlinear changes of signals, summation (processes of induction), and subtraction (processes of inhibition) of signals. As the mechanism of formation of these relationships, a scheme analogous to that which I used to explain the formation of chromaticity signals can therefore be suggested: a secondary logarithmic operation on the signals followed by their paired subtraction:

$$\begin{aligned}V_{\alpha\beta} &= V'_\alpha - V'_\beta = \log V_\alpha - \log V_\beta = \log \frac{V_\alpha}{V_\beta}, \\ V_{\beta\gamma} &= V'_\beta - V'_\gamma = \log V_\beta - \log V_\gamma = \log \frac{V_\beta}{V_\gamma}, \\ V_{\gamma\alpha} &= V'_\gamma - V'_\alpha = \log V_\gamma - \log V_\alpha = \log \frac{V_\gamma}{V_\alpha}.\end{aligned}$$

Since information concerning the color hue is unidimensional, the signals $V_{\alpha\beta}$, $V_{\beta\gamma}$, and $V_{\gamma\alpha}$ characterize it very excessively. It is easy to show that all these signals are dependent on one variable, characterizing the color hue, and they are therefore interconnected by simple relationships.

It is interesting to note that the suggested scheme of analysis of color information by the retina (Fig. 4) is based on the principle of parallel processing of signals in different channels in the presence of an overall excess, and it includes the consecutive repetition of analogous operations performed by simple elements. In this respect the scheme has much in common with the suggested structure of the brain reflected in Rosenblatt's percentrons [6].

/17

7. Verification of the suggested model of the process of color identification must be carried out by comparing its output signals with the corresponding results of psychophysical experiments. It must always be remembered, when this

is done, that the experiments were performed on the real eye under complex conditions of observation, but during construction of the model, a number of simplifications were introduced into the mechanism of identification.

The surfaces of constant values of luminosity, color hue and saturation, which have a simple shape in the color space of sensations (Fig. 7), are transformed into the ordinary color space RGB (or the MKO—XYZ space) into surfaces of complex shape. Under these circumstances the identification of these surfaces will depend on laws of nonlinearity of the primary receivers, which in turn are determined by the conditions of adaptation, and also on values of the constant coefficients included in the relationships. Preliminary calculations by the writer have demonstrated a close correlation between the surfaces of constant saturation and color hue obtained by calculation and the experimental data in accordance with Maxwell's system. It is important to note that the suggested model explains certain general principles of the process of color vision: independence of chromaticity thresholds of the brightness level and independence of brightness thresholds of the chromaticity level (with strictly logarithmic functions), the Abney and Bezold—Bruecke phenomena. On the basis of the mathematical model described above, an electronic analog model of the identification process has been built and tested. This model can be used to determine the type of functional relationships and optimal values of the constant coefficients which are most appropriate to psychophysical experiments under different conditions of observation.

The writer is grateful to S.A. Brenzen, who took part in the work of this investigation, and to Z.I. Tkacheva, for her help with the calculations and graphs.

REFERENCES

1. Nyuberg, N.D. Z. Phizik. 52, 406, 1928.
2. Nyuberg, N.D. Probl. Fiziol. Optiki 9, 61, 1950.
3. Nyuberg, N.D. Dokl. Akad. Nauk SSSR 50, 143, 1945.
4. Nyuberg, N.D. and Ye.N. Yustova. Trud. Gos. Opt. Inst. 24, 143, 1955.
5. Orlov, O.Yu. and Ye.N. Maksimova. Vision Research 5, 573, 1965.
6. Rosenblatt, F. Printsipy neyrodinamiki (Principles of Neurodynamics), Mir Press, Moscow, 1966.
7. Rymov, A. I. and D.A. Shklover. Author's Certificate No. 158107, 1961. 18
8. Rymov, A. I. Svetotekhnika (Light Engineering) 11, 20, 1965.
9. Shklover, D.A. Izvest. Akad. Nauk SSSR, Ser. Fiz. 13, 275, 1949.
10. Shklover, D.A. Tezisy 4-go soveshchaniya po fiziologicheskoy optike (Proceedings of the 4th Conference on Physiological Optics), Leningrad, 23, 1954.
11. Shklover, D.A. Vision Problems of Color 2, 603, 1958.
12. Shklover, D.A. Author's Certificates Nos. 102851 and 106027, 1954.
13. Adams, E.Q. Journ. Opt. Soc. Amer., 31, 168, 1942.
14. Brown, P.K. and G. Wald. Science 144, 45, 1964.
15. De Valois, R.L. Optic, 20, 87, 1963.
16. Friel, F. Die Farbe (Color), 10, 193, 1961.
17. Hartline, H.K. Amer. Journ. Physiol. 121, 400, 1938.
18. Hering, E. Lehre vom Lichtsinn (Perception of Light), Berlin, 1920.
19. MacAdam, O. Vision Research, 1, 9, 1961.

20. MacNichol, E.F. Vision Research, 4, 119, 1964.
21. Richards, W. Journ. Opt. Soc. Amer., 56, 1110, 1966.
22. Stevens, S.S. Journ. Opt. Soc. Amer., 53, 375, 1963.
23. Sinden, R.H. Journ. Opt. Soc. Amer., 28, 339, 1938.
24. Stails, W.S. Pros. Phys. Soc., 58, 41, 1946.
25. Wald, G. Science, 145, 1007, 1964.

All-Union Research Institute of Illumination Engineering
Moscow, USSR

CERTAIN PSYCHOPHYSIOLOGICAL PRINCIPLES OF COLOR PERCEPTION DESCRIBED BY A NONLINEAR MODEL

A. V. Matveyev

Description of a mathematical model of human vision based on the spectral sensitivity curves of three color-sensitive receivers (green, red, and blue). Analysis of the model's equations shows that the curves for the dependence of perception on color are more linear for the red and green receivers than for the blue receiver. All achromatic tints are positioned along a hyperbola in perception space, bending toward the axis of the blue receiver.

Overcoming the "tragic discrepancy" between colorimetric and psychophysiological ideas of color, to use N.D. Nyuberg's words, is an extremely difficult task, bearing in mind that the unknown functional link between the color stimulus and the sensation it produces depends on many factors. The ambivalence of the relationship between sensation and stimulus is the reason why color perception can remain constant under different conditions of observation.

/ 19

Since the character of the functional relationships is determined not only by inadequately studied principles of transformation of radiant energy into nervous excitation, but also by complex processes of analysis of color information by the central parts of the visual system, it is necessary to use Ashby's "black box" method to solve the problem. By means of this method a simulated relationship between different functions obeying mathematical logic can be described. The problem can be reduced to the degree to which, and the limits between which, the resulting behavior of the mathematical model coincides with the experimental data obtained by different workers.

In the model I have developed [1, 2] I started out from the concept of color perception as a three-dimensional magnitude, describable by a point in color perception space. The position of this point is determined by three nonlinear hyperbolic functions for three receptors, allowing for the stimulus of adaptation:

$$v_m = A_m \frac{m'}{a_m m' + m'_a},$$

where $m' = \begin{bmatrix} r' \\ g' \\ b' \end{bmatrix}$, $m'a = \begin{bmatrix} r'a \\ g'a \\ b'a \end{bmatrix}$ are values of the stimuli characterizing the investigated color and the color of adaptation in the physiological system; A_m is a coefficient proportional to the sensitivity of the m -th receptor; and α is a coefficient allowing for nonlinearity of the response of the receptor.

The luminosity, saturation, and achromatic axis under these circumstances are arbitrary concepts, which reflect, not so much their physiological as their psychophysiological nature. Because of the nonlinearity of the transformation, it can be based only on the physiological system. For this reason, in the model I have developed, the principal colors chosen were those of Nyuberg and Yustova [3] because under these circumstances the curves of addition are closest to the spectral sensitivity curves of the receptors, as the experiments of MacNichol and Wald [7, 9] have confirmed.

/20

The equations were standardized in accordance with the classical work of MacAdam [6]. It is interesting to note that the mean geometric deviation of the major and minor half-axes of the ellipses from the mean radius of the circles (Fig. 1) is 24%. This is 1.5 times less than for the equal-contrast graph of MacAdam recommended by the International Commission on Illumination for the assessment of color differences. On the basis of the resulting equations, changes in the threshold of color hue and saturation were determined for homogeneous radiations [2], and these agreed satisfactorily with the known experimental data obtained by several workers.

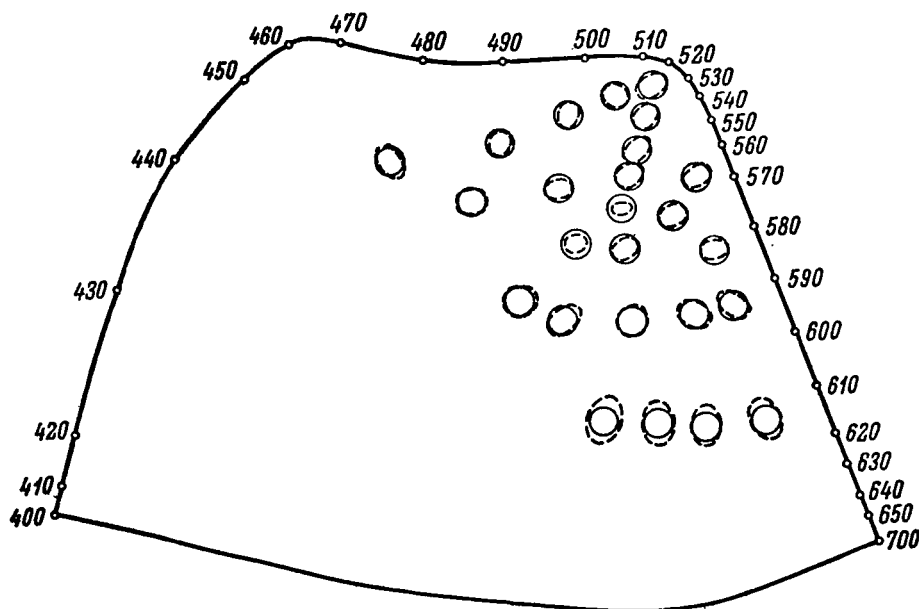


Figure 1. MacAdam's Threshold Ellipses During Scanning of a Surface of Uniform Brightness. Numbers on Graph Denote Wavelengths in $m\mu$. Explanation in Text.

Wyszecki and Wright [10] compared color differences obtained theoretically with the experimental data of Wright and Sugiyama. From the published material, similar comparison can be made between my model and Wright and Sugiyama's three series of experiments. In the suggested model, color discrimination is determined by the distance between two points characterizing the colors to be investigated:

$$\Delta S = [\sum m (\Delta \nu_m)^2]^{1/2},$$

where $\Delta \nu_m$ denotes the difference between coordinates of color perception in the system ν_m .

On the basis of this equation, N. M. Belyayeva calculated theoretical color differences ΔS from Wright and Sugiyama's data for ratios between brightnesses of object and adaptation stimulus of 2.8 for the first experiment and 3.0 for the other two. The results of her calculations are shown on graphs (Figs. 2, 3 and 4) in which color differences obtained experimentally by Wright and Sugiyama are plotted along the axis of ordinates and the calculated values along the axis of abscissas. The straight line with a slope of 45° corresponds to ideal coincidence between experiment and calculation. The two other straight lines correspond to differences of 25% between the theoretical and experimental values. Unfilled circles correspond to Wyszecki's calculations.

/21

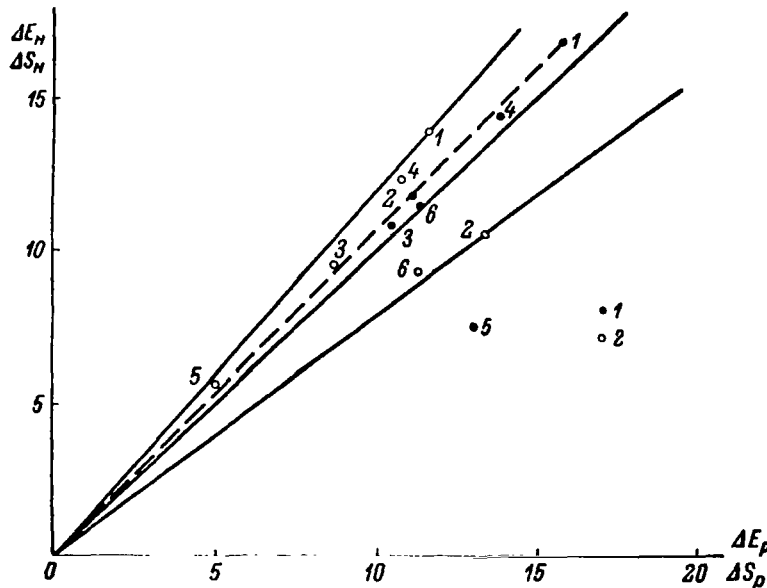


Figure 2. Observed and Calculated Color Differences for Five Pairs of Colors (Series 1 of Wright's Experiments). Numbers near Curves Identify Colors. 1 - In System ν_r , ν_g , ν_v ; 2 - in UVW System. Remainder of Explanation in Text.

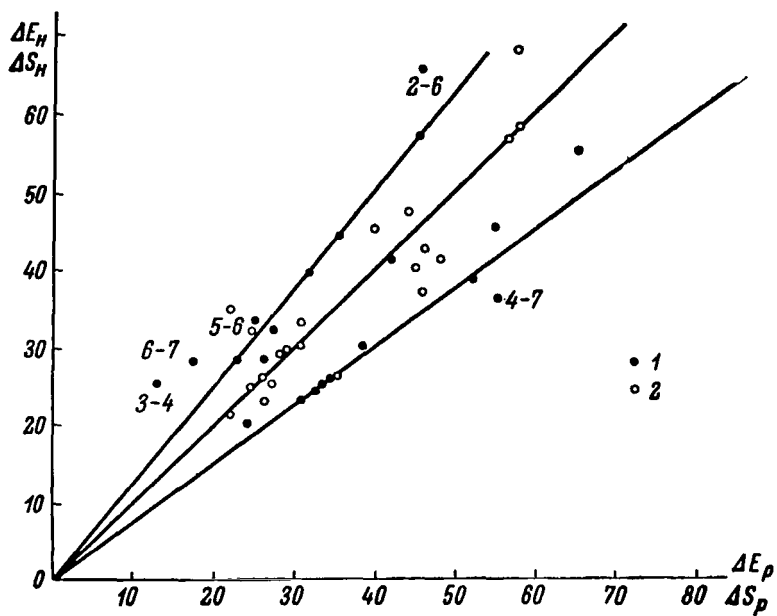


Figure 3. Observed and Calculated Color Differences for 22 Pairs of Colors (Series 2 of Wright's Experiments). Legend as in Fig. 2.

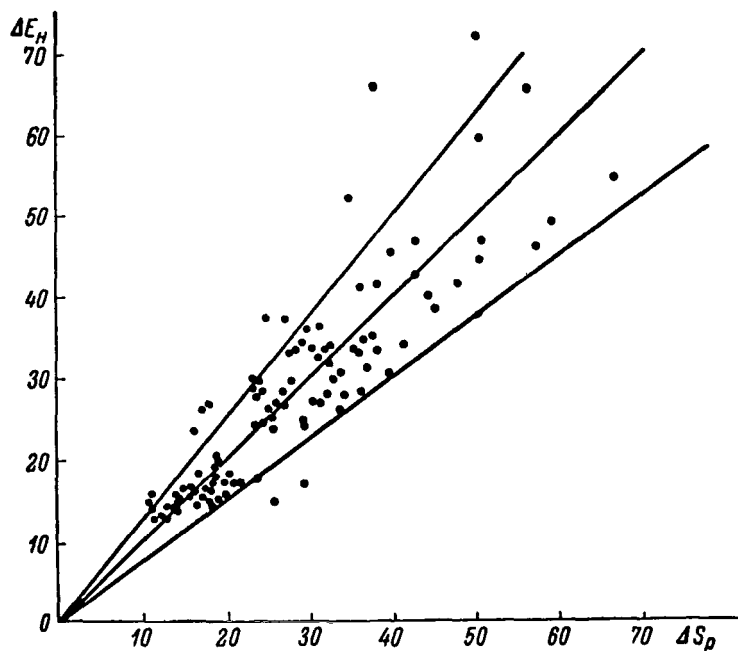


Figure 4. Observed and Calculated Color Differences for 117 Pairs of Colors (Series 3 of Wright's Experiments). Legend as in Fig. 2.

/22

As the graphs show, Wyszecki's and my own calculated data agree with the experimental observations with an accuracy of 25%, corresponding approximately to the accuracy of the experimental method used by these workers.

Analysis of the equations showed that deviations from the linear relationship differed for receptors sensitive to different colors. For example, the relationship between sensation and stimulus for red and green receptors is closer to linear than the corresponding relationship for the blue receptor. As a result of this asymmetry the nature of which is not yet clear, all colors achromatic from the colorimetric point of view were situated in the space of sensations, not on a straight line, but on a hyperbola convex toward the axis of the blue receptor. Under these circumstances, a color displaced from colorimetric white toward the blue receptor must be perceived as white.

Displacement of a white point from its colorimetric value at different brightnesses was demonstrated experimentally many years ago by Helmholtz [5]. In the first experiment white light was obtained by optical displacement of violet and yellow-green homogeneous radiation, and in the second by displacement of indigo and yellow. It is interesting to note that Helmholtz observed the largest displacement in the second case, but in experiments with other complementary colors, the displacements could not be measured. Explanation of this phenomenon is based on a nonlinear relationship between sensation and stimulus.

Recently, at the All-Union Research Institute of Illumination Engineering, detailed measurements have been made of thresholds close to the point of white light for white objects against a gray background. The threshold ellipse plotted from data for 7 observers, taken from A.I. Rymov's dissertation, is shown in Fig. 5. The center of the ellipse is displaced toward Nyuberg's triangle, i.e., toward the basic blue color of the physiological system.

/23

The writer has determined the curvature of the achromatic axis experimentally in a special system illustrated in Fig. 6. A white square object [4] with angular dimensions of $5 \times 5^\circ$ was shown to an observer against a background [3] with a luminance of 10 nit, uniformly illuminated by projectors [2 and 6]. The object was illuminated by a project or [1] with a long-focus objective, inside which was placed a frame with two filters. The filters, blue and yellow, were chosen so that as a result of movement of the frame, the chromaticity of the object changed in the direction of the basic blue color of the physiological system. The luminance meanwhile remained constant. A screen [5] protected the object against rays of light from the sources of illumination.

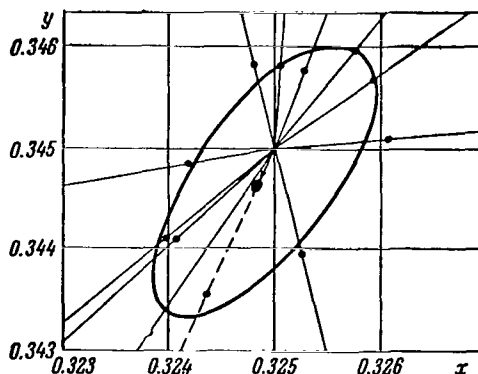


Figure 5. Threshold near White Point from A.I. Rymov's Data (All-Union Research Institute of Illumination Engineering).

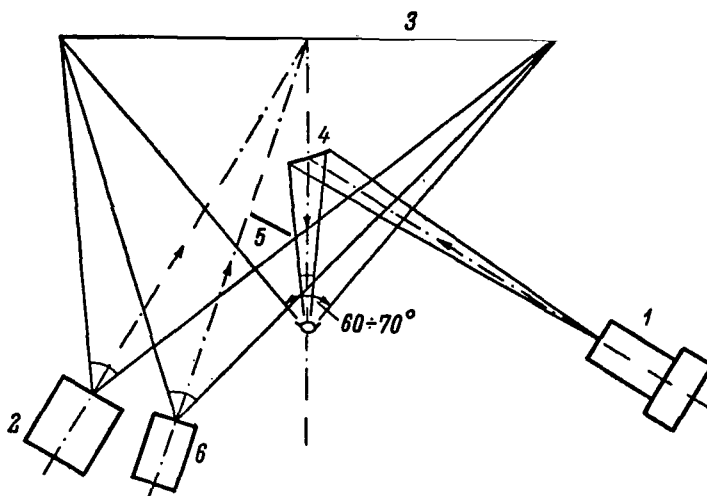


Figure 6. Scheme of Experimental Situation. Explanation in Text.

The position of the white point for different ratios between luminance of object and background was determined by the method of presentations. The observer had to state how he saw the object: whether as blue or yellow. The experimental results were subjected to statistical analysis by the probit method, on the basis of "normality" of the effect curve, and allowing for confidence limits calculated for the given frequency of discovery. The white point was determined with a 50% level of probability. Five subjects took part in the experiments.

/24

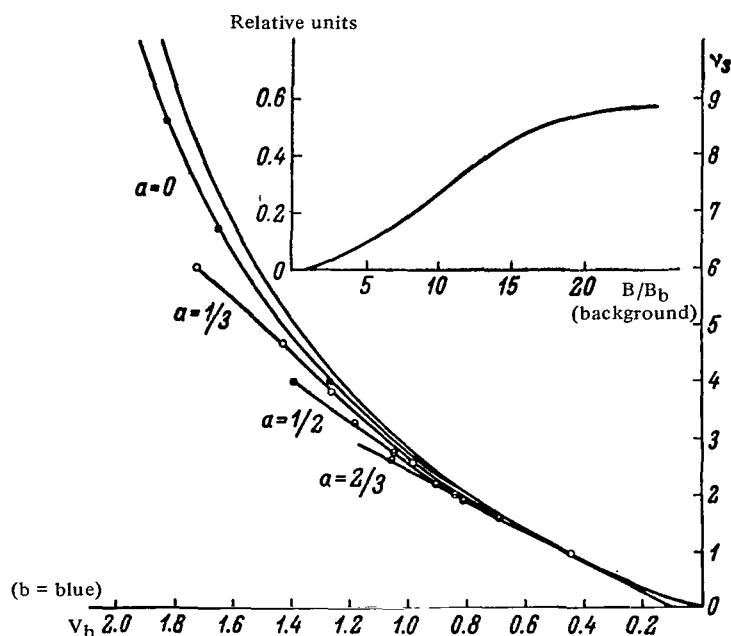


Figure 7. Displacement of Point of White Light as a Function of Ratio Between Luminances of Object and Background and Curvature of Achromatic Axis. Explanation in Text.

The averaged results for five observers are shown as a relationship of the shift of chromaticity of the white point to the ratio between luminances of object and background (Fig. 7). The greatest shift observed, with a ratio of 20:1 between the luminances of object and background, corresponds to a change in the coordinates of chromaticity Δx , Δy of 0.02. The projection of the achromatic axis on the plane of coordinates ν_b , ν_g is also shown here. The points denote experimental data plotted on the graph in accordance with hypothetical functions describing the relationship between adaptation stimulus and object stimulus. As the writer has previously pointed out [1], this relationship must hold good for object luminances considerably in excess of background luminance. Power relationships between the adaptation stimulus and the ratio between object and adaptation stimuli were investigated. The experimental results are plotted for different values of the power a . As the graph (Fig. 7) shows, the experimental data correspond closely to a straight line for a power of $2/3$. The power value of the relationship thus obtained is higher than the power value of the corresponding relationship obtained by Bodman for luminosity ratios [4]. It is difficult at present to give a precise relationship between adaptation stimulus and various factors, but even at this stage the important role of this parameter in color perception can be discerned.

/25

It is interesting to note the effect of a change in chromaticity of adaptation on the character of color perception in this model. Calculations made for three values of the adaptation stimulus, corresponding to the color of three standard sources of white light A, B, and C, showed that the shape of the locus on a surface of equal brightness changes extremely slightly (the changes affect mainly the region of blue-green radiations). This fact suggests that only slight changes take place in color perceptions during a change in the adaptation stimulus, i.e., that color sensations are constant.

Measurement of shifts of the white point can be used to plot the axis of white colors in a space of color sensations as the tangent to the curve of achromatic colors. This new position of the axis will determine the psychophysiological characteristics of the color: luminosity, color hue, and saturation. In particular, one result of shifts in the white point is a shift in the black point from the origin of the coordinates to the point whose coordinates are $(0, 0, \nu_{00})$. For this reason the origin for counting luminosities does not coincide with the origin of the coordinates for the space of sensations. This discrepancy provides an explanation for the eccentricity of closed curves of equal ratios of luminosity to luminance and the white point on the International Commission on Illumination graph obtained experimentally by Sanders and Wyszecki [8].

Theoretical curves for equal ratios between luminosity and luminance obtained by intersection of spherical surfaces of equal luminosity with surfaces of equal luminance are given in Fig. 8. The ratio between luminosity and luminance of achromatic colors is taken as unity. It must be pointed out that for yellow colors this ratio is less than unity, in agreement with the experiments of Sanders and Wyszecki. However, compared with the results obtained by these workers, the calculated curves of equal values of luminosity/luminance ratio are displaced slightly toward the red part of the locus, a fact which is explained by the insufficiently accurate choice of $A_r:A_g$ ratio in the equation of the equal-contrast space.

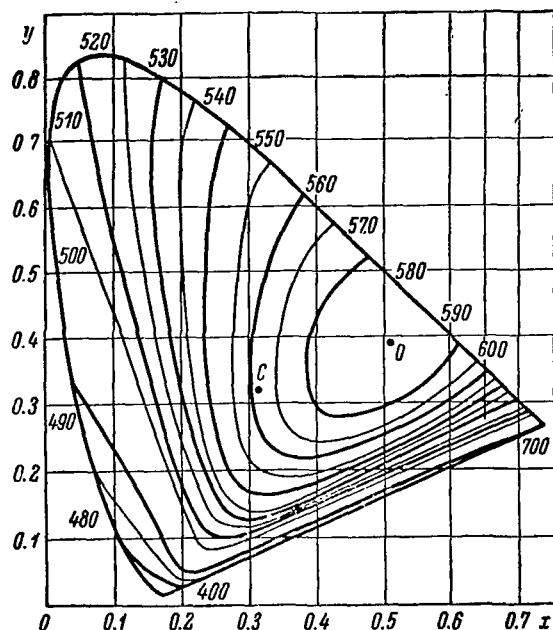


Figure 8. Family of Chromaticities with Equal Ratios of Luminosity to Luminance. Explanation in Text.

SUMMARY

1. A model of color perception based on hyperbolic relationships between sensation and stimulus can be used to describe a number of the chief psychophysiological phenomena of color perception (the Bezold—Abney effect, dependence of saturation and color hue threshold as a function of wavelength), and also to assess color discrimination.

/26

2. Analysis of the equations of the model has shown that deviations from a linear relationship for the blue receptor are greater than those for red and green, as a result of which all colors which are achromatic from the colorimetric point of view were located in the space of sensations, not on a straight line, but on a hyperbola, convex toward the axis of the blue receptor.

3. Displacement of the white point from its colorimetric value, measured on a special apparatus, has been used to determine the curvature of the achromatic axis.

4. Analysis of the curvature of the achromatic axis permitted an empirical relationship to be deduced between the adaptation stimulus and object stimulus and the coordinates of the black point (the origin for counting luminosities) to be established.

5. On the basis of the definition of luminosity as distance from the black point, relationships reflecting the "flaming" of colors (the Helmholtz—Kohlrausch effect) have been obtained.

REFERENCES

1. Matveyev, A.B. Svetotekhnika (Light Engineering), 12, 15, 1964.
2. Matveyev, A.B. Svetotekhnika (Light Engineering), 9, 1, 1965.
3. Yustova, Ye.N. Probl. Fiziol. Optiki (Problems of Physiological Optics), 8, 112, 1953.
4. Bodman, H.W. Lichttechnik (Light Engineering), 8, 1962.
5. Helmholtz, H. Handbuch der Physiologischen Optik (Handbook of Physiological Optics), Vol. 2. Hamburg and Leipzig, 1911.
6. MacAdam, D.L. J. Opt. Soc. Amer. 32 5, 48, 1942.
7. MacNichol, E.F. Scient. Amer. 211, 6, 1964.
8. Sanders, C.L. and G. Wyszecki. J. Opt. Soc. Amer. 48 6, 389, 1958.
9. Wald, G. Science 145, 1007, 1964.
10. Wyszecki, G. and W.D. Wright. J. Opt. Soc. Amer. 55, 1166, 1965.

Department of Illumination Engineering and Light Sources
Moscow Institute of Energetics

DEDUCTIVE CONSTRUCTION OF A MODEL FOR THE LOWER METRIC OF COLOR

Yu. P. Shabanov-Kushnarenko

Presents a new, logically-equivalent formulation of
Grassman's laws without using color composition operations.

Schrödinger [7] pointed out that it was possible to derive a model of vision statics from Grassman's laws [4]. But the derivation given by him for the model contains a logical error. The fact is that the formulation of Grassman's laws adopted by Schrödinger uses the operation of color composition. At the same time, however, the legality of introducing this operation can be rigorously justified only by resorting to a model of vision statics.

/27

Presented in the present paper is a new formulation of Grassman's laws in which the operation of color composition is not used and in which the logical equivalence of a model of vision statics to Grassman's laws as newly formulated is proven.

1. FORMULATION OF THE MODEL OF VISION STATICS

On the basis of the studies of Newton [3], Young [8], Maxwell [6] and Helmholtz [5], the model of vision statics can be formulated as follows:

$$U_i = \int_{\lambda_1}^{\lambda_2} E(\lambda) \cdot A_i(\lambda) \cdot d\lambda, \quad (i = 1, 2, 3), \quad (1)$$

$$B = f(U), \quad (2)$$

where λ is the radiation wavelength, varying in the interval $[\lambda_1, \lambda_2]$,

$E(\lambda)$ is the spectral intensity of the radiant energy of the radiation perceived by the eye;

$A_i(\lambda)$ are fixed, linearly independent, everywhere bounded functions (functions of composition by the eye);

U_i are the colorimetric coordinates of the color; U is the color vector with the color coordinates U_1, U_2, U_3 ;

B is the vector of color sensation;

f is a one-to-one vector-function.



2. FORMULATION OF GRASSMAN'S LAWS

Let the radiation $E'(\lambda)$ and $E''(\lambda)$ be formulated on the comparison fields presented to the observer in an experiment. For the characteristics of the experimental conditions we introduce the function

$$E(\lambda) = E'(\lambda) - E''(\lambda). \quad (3)$$

Grassman's laws are formulated as follows.

/28

1st law. If the colors of the comparison fields are observed to be the same in two experiments with conditions characterized by the functions $E_1(\lambda)$ and $E_2(\lambda)$, the colors of the comparison fields will also be found to be the same in all possible experiments with conditions characterized by the function $E_1(\lambda) + E_2(\lambda)$.

2nd law. There exists a set of three fixed functions $E_1(\lambda)$, $E_2(\lambda)$, $E_3(\lambda)$ in which we can find, in fact, uniquely, for any function $E(\lambda)$ a set of three real numbers U_1 , U_2 , U_3 such that the colors of the comparison fields will be found to be the same in experiments with conditions characterized by the function

$$U_1 E_1(\lambda) + U_2 E_2(\lambda) + U_3 E_3(\lambda) + E(\lambda),$$

3rd law. Continuous variation of the numbers U_1 , U_2 , U_3 corresponds to a continuous variation of the function $E(\lambda)$.

Despite its awkwardness, Grassman's laws as here formulated admit of direct experimental verification.

3. EQUIVALENCE OF THE MODEL OF VISION STATICS AND GRASSMAN'S LAWS

From Grassman's laws follows the validity of formulas (1) and (2). In fact, the ensemble of functions $E(\lambda)$, which are the spectral difference of pairs of all-possible radiations, forms a linear normalized space $\bar{L}[\lambda_1, \lambda_2]$ of summable functions. Moreover, the numbers U_1 , U_2 , U_3 introduced by Grassman's second law are linear continuous functionals of the function $E(\lambda)$. The additivity of these functionals is easily proved on the basis of the first and third laws of Grassman.

According to the theorem on the general form of a functional [1], the functionals U_1 , U_2 , U_3 have form (2), where $A_1(\lambda)$, $A_2(\lambda)$, $A_3(\lambda)$ are fixed functions, bounded almost everywhere. The linear independence of these functionals can be proved on the basis of the first and second laws of Grassman.

Finally, resorting to the first two laws of Grassman it can be proved that:
1) radiations having the same values of functionals (2) generate the same colors;
2) radiations generating identical colors have identical values of the functionals (2). This proves the validity of relation (2).

The reverse derivation of Grassman's laws from the model of vision statics is trivial and does not contain any difficult moments.

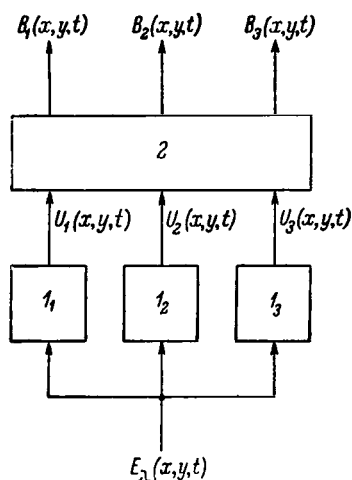
4. GENERALIZATION OF THE MODEL

The model of vision statics represented by formulas (1) and (2) can be generalized to the case of dynamics, when the observer is presented with visual patterns that vary arbitrarily both in time t and in visual field x, y . To this end Grassman's laws should be supplemented by the following postulate.

Visual sensation $B(x, y, t)$ will remain the same if the radiations in the visual pattern $E_\lambda(x, y, t)$ generating this sensation are replaced arbitrarily by any other metameric radiations.

Substantial use was made in the formulation of this postulate of Nyuberg's idea on the substitution of metameric radiations [2].

/29



Generalized Model of Vision (Diagram). Explanation in the Text.

The generalized model of vision can be represented in the form of the scheme illustrated in the figure.

The function of the blocks 1_i ($i = 1, 2, 3$) and 2 is described by the following relations:

$$U_i(x, y, t) = \int_{\lambda_1}^{\lambda_2} E_\lambda(x, y, t) \cdot A_i(\lambda) \cdot d\lambda, \quad (3)$$

$$B(x, y, t) = F[U(x, y, t)], \quad (4)$$

where $E_\lambda(x, y, t)$ is the radiation spectrum, specified for any instant of observation t at any point of the field of vision with coordinates x, y ;

$B_1(x, y, t)$ is a three-component vector-function of visual sensation;

$B_i(x, y, t)$ are the components of visual sensation;

F is a single-valued operator.

REFERENCES

1. Lyusternik, A.A. and V.I. Sobolev. *Elementy funktsional'nogo analiza* (Elements of Functional Analysis), Nauka Press, Moscow, 1965.
2. Nyuberg, N.D. Grassman's laws, in the book: *Fizicheskiy entsiklopedicheskiy slovar'* (Physical Encyclopedic Dictionary), Moscow, 1966.
3. Newton, I. *Optika* (Optics), Gostekhteorizdat, Moscow, 1954.

4. Grassman, H. Zur Theorie der Farbenmischung (On the Theory of Color Mixing), Ann. Phys. 1853.
5. Helmholtz, H. Handbuch der physiologischen Optik (Handbook of Physiological Optics), Hamburg and Leipzig, 1909-1911.
6. Maxwell, J. C. On the Theory of Compound Colour and the Relations of the Colours of the Spectrum, Proc. Roy. Soc., 10, 910, 1860.
7. Schrödinger, E. Die Gesichtsempfindungen (Visual Perception), Lehrbuch der Physik, Mueller-Poillet, Ed., Vol. 2, 1926.
8. Young, T. Lecture on the Theory of Colours, Phil. Trans. Roy. Soc., 21, 1802.

Chair of Mathematical Simulation
Kharkov Institute of Radio Electronics

OPERATOR ANALYSIS OF ELECTRORETINOGRAMS

D. S. Melkonyan and L. G. Barsegyan

It is shown that within certain frequency and illumination ranges, the light stimulus and the resulting potential are related by a function that can be described by a linear stationary operator, which is derived from an experimentally-determined APFC function.

30

In electrophysiological studies of the visual system one of the indicators of the functional state of its structures are the potentials elicited by stimuli whose parameters can be varied within broad limits. The problems of the choice of stimuli and of analysis of the potentials evoked by them are intimately connected; in particular, perfected methods of analysis can reduce the number of stimuli required for the study and a rational choice of stimuli can simplify the analysis.

Presented in this paper is an operator analysis of the elicited potentials. This is an analysis based on a mathematical model describing the relationship between the stimulus and the potential it evokes using a linear stationary operator. The application of certain methods of the theory of a Fourier integral to the model under consideration establishes a relationship between the potentials elicited by various stimuli and permits combination of the choice of stimuli and analysis of the potentials evoked by them in such a way as to obtain the maximum quantity of data characterizing the system.

The question as to how successful an approximation to the actual processes the proposed mathematical model is can be solved only by an experimental approach. For this reason the theoretical hypotheses are illustrated by the experimental data obtained by recording the electroretinograms (ERG) of a person in response to light stimuli.

MATHEMATICAL MODEL

In view of the present status of knowledge regarding the physicochemical processes occurring in structures of the visual system, a complete mathematical description of the system is unreal. But it is possible to attempt to trace the interrelationship between certain phenomena by means of mathematical models. It is this type of model that is examined below; the stimulus and the potential it evokes are chosen for the study. The form of the stimulus, the way it is applied and the point of deriving the potential in large measure determine the parameters

of the mathematical model, but have no influence whatever on the generality of the theoretical considerations.

Representing the stimulus and the evoked potential in the form of time functions $x(t)$ and $y(t)$, respectively, where t is the running time, we write the relationship between them as

$$y(t) = T\{x(t)\}, \quad (1)$$

where T is an operator.

An operator is a specific law by which one numerical sequence is associated with another. Of special interest are operators having the properties of being linear and stationary, since they can be used for purposes of harmonic analysis, as was done by Weiner [3].

31

A stationary operator is characterized by the fact that a shift in time without a change in the form of the function $x(t)$ leads to the same shift in time of the function $y(t)$, also without a change in its form. The property of being stationary requires fulfillment of the following conditions: if $x(t + \tau) = x_1(t)$, $y(t + \tau) = y_1(t)$, $T\{x(t)\} = y(t)$, then $T\{x_1(t)\} = y_1(t)$.

We will assume that the property of being stationary is possessed by an operator describing one of the states of the visual system and that different states are described by a family of stationary operators. In the case being examined, therefore, the property of being stationary reduces to the following assertion: for identical states of the visual system identical and identically applied stimuli evoked equivalent potentials when derived from at the same point. In practice, it is difficult to determine that states of the visual system are identical, due to the necessity of accounting for a tremendous number of factors. This is precisely why a stationary operator is an approximate description of the states of the visual system that can be considered identical with some degree of precision.

An operator is said to be linear if the following conditions are fulfilled:

$$\begin{aligned} T\{x_1(t) + x_2(t)\} &= T\{x_1(t)\} + T\{x_2(t)\} \\ T\{a \cdot x(t)\} &= a \cdot T\{x(t)\}, \end{aligned} \quad (2)$$

where a is a constant. A linear stationary operator will be denoted by L .

Fourier Integral Method. Consider the effect of a linear stationary operator on the exponential function

$$L\{e^{j\omega_k(t+\tau)}\} = e^{j\omega_k\tau} L\{e^{j\omega_k t}\}, \quad (3)$$

where $j = \sqrt{-1}$ and ω_k is some fixed value of the angular frequency.

From (3) with $t = 0$ we get

$$L\{e^{j\omega_k\tau}\} = S(j\omega_k) \cdot e^{j\omega_k\tau}, \quad (4)$$

where $S(j\omega_k) = L\{e^{j\omega_k t}\}$ when $t = 0$.

Thus, application of the linear stationary operator L to the function $e^{j\omega_k t}$ reduces to multiplying it by the complex number $S(j\omega_k)$, which depends only on the properties of the operator and on the angular frequency ω_k . Determining the value of $S(j\omega_k)$ for a continuous series of frequencies ω_k from zero to infinity, we get a function of the complex variable $S(j\omega)$ having the following forms:

$$S(j\omega) = S(\omega) \cdot e^{j\delta(\omega)} = P(\omega) + jQ(\omega), \quad (5)$$

where $S(\omega) = |S(j\omega)|$ is the modulus and $e^{j\delta(\omega)}$ the argument. $P(\omega) = \operatorname{Re}[S(j\omega)]$ and $Q(\omega) = \operatorname{Im}[S(j\omega)]$ are the real and imaginary parts of the function of the complex variable $S(j\omega)$.

In automation, $S(\omega)$ usually denotes the amplitude frequency characteristic, δ the phase frequency characteristic and $S(j\omega)$ the amplitude-phase frequency characteristic (APFC) [5].

If $x(t)$ is a physically realizable function, it can be written by means of the Fourier integral as

$$x(t) = \frac{1}{2\pi} \int_{-\infty}^{\infty} X(j\omega) e^{j\omega t} d\omega, \quad (6)$$

where

$$X(j\omega) = \int_{-\infty}^{\infty} x(t) e^{-j\omega t} dt. \quad (7)$$

The complex function $X(j\omega)$ is usually called the complex spectrum [3] of the function $x(t)$.

The integrand in Eq. (6) consists of terms of the form $[X(j\omega) d\omega] e^{j\omega t}$, that is, an infinite number of functions $e^{j\omega t}$ with infinitely small complex amplitudes $X(j\omega) d\omega$ is integrated. The action of the operator L on the harmonic function $e^{j\omega_k t}$ reduces to multiplication by the complex number $S(j\omega_k)$. Owing to this circumstance, we can find the effect of the operator on the stimulus $X(t)$, represented in the form of (6),

$$\begin{aligned} y(t) &= L\{x(t)\} = L\left\{\frac{1}{2\pi} \int_{-\infty}^{\infty} X(j\omega) e^{j\omega t} d\omega\right\} = \\ &= \frac{1}{2\pi} \int_{-\infty}^{\infty} X(j\omega) S(j\omega) e^{j\omega t} d\omega = \frac{1}{2\pi} \int_{-\infty}^{\infty} Y(j\omega) e^{j\omega t} d\omega, \end{aligned} \quad (8)$$

where

$$Y(j\omega) = X(j\omega) S(j\omega) \quad (9)$$

is the complex spectrum of the function $y(t)$. On the basis of expression (8), a relation can be found between $x(t)$ and $y(t)$ by means of the APFC, $S(j\omega)$, that can be determined experimentally.

EXPERIMENTAL DETERMINATION OF THE FREQUENCY CHARACTERISTICS

In experimental determination of frequency characteristics it is necessary to combine the choice of stimuli and the analysis of the evoked potentials in such a way as to find $S(j\omega)$ from the experimentally determined $x(t)$ and $y(t)$. On the basis of (9) the general method of solving this problem is determined by the formula

$$S(j\omega) = \frac{Y(j\omega)}{X(j\omega)} = \frac{\int_{-\infty}^{\infty} y(t) e^{-j\omega t} dt}{\int_{-\infty}^{\infty} x(t) e^{-j\omega t} dt}, \quad (10)$$

i.e., the APFC of a system described by a linear stationary operator can be determined as the ratio of the complex spectra of the functions $y(t)$ and $x(t)$. In some studies [4] an experimental method is described for determining the frequency characteristics using sinusoidally modulated light stimuli. Let us present the foundations for this method by means of the proposed mathematical model.

Let the stimulus $x(t) = \cos \omega_k t = R_e[e^{j\omega_k t}]$; then the evoked potential, on the basis of (4), is

$$\begin{aligned} y(t) &= R_e[S(j\omega_k) \cdot e^{j\omega_k t}] = R_e[S(\omega_k) \cdot e^{j(\omega_k)} \cdot e^{j\omega_k t}] = \\ &= S(\omega_k) \cdot \cos[\omega_k t + \delta(\omega_k)]. \end{aligned} \quad (11)$$

According to this expression (11), when a sinusoidally varying stimulus is applied to the input of a system described by the operator L , the potential also must change sinusoidally. This property can be used to verify the linearity and stationarity of the system being studied. Of great value is the fact that the check can be made at different frequencies. At the angular frequency ω_k the ratio of the amplitude of the evoked potential to the amplitude of the stimulus yields the point of the amplitude frequency characteristic $S(\omega_k)$, and the angle of shift between the sinusoids, $\delta(\omega_k)$, yields the point of the phase frequency characteristic.

Thus, using sinusoidal stimulation and finding $S(\omega_k)$ and $\delta(\omega_k)$ for a broad range of frequencies, we can determine experimentally the amplitude frequency characteristic $S(\omega)$, the phase frequency characteristic $\delta(\omega)$ and the APFC

/33

$S(j\omega) = S(\omega) e^{j\delta(\omega)}$, imaged on the complex plane. The plot of the APFC point corresponding to the angular frequency ω_k is shown in Fig. 1.

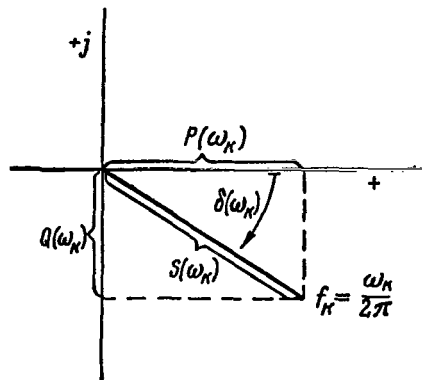


Figure 1. Plot of the APFC Point Corresponding to the Angular Frequency ω_k . Symbols Explained in the Text.

METHOD

One of the objectives of our experimental research was to verify the properties of linearity and stationarity in the human retina and to clarify the possibility of using frequency characteristics for diagnostic purposes.

The person being examined was placed in a shielded light- and soundproof chamber. After five minutes of dark adaptation a light flux was applied from a lamp with a continuous radiation spectrum, focused onto the pupil by an optical system. The path of the light beam was interrupted by the rim of a disk with perforations, designed so that when the disk was rotated at the angular frequency ω_k the illumination on the pupil, $E(t)$, varied according to the law

$$E(t) = E_m [1 + \sin(\omega_k t + \psi)], \quad (12)$$

where E_m is a constant component of the illumination, ψ is an angle depending on the instant chosen as the start of the time count.

The ERG was recorded as the difference in potentials

$$U_{an}(t) = \varphi_a(t) - \varphi_n(t), \quad (13)$$

where $\varphi_a(t)$ is the potential evoked from the cornea of the eye being studied (active electrode) and $\varphi_n(t)$ is the potential evoked from the ear lobe (passive electrode). Used as the active electrode was a modified contact lens with an

opening in the center and an inserted platinum electrode. The difference in potential $U_{an}(t)$ and the voltage of the F-102 photocell, proportional to $E(t)$, were amplified by means of a 4EEG-1 electroencephalograph and were recorded on an H-700 oscillograph. The use of this oscillograph permitted recording of the quantities under study with a considerable time and amplitude scan (the width of the photographic paper was 12 cm; the feed rate was from 16 to 250 cm/sec).

EXPERIMENTAL DATA

Given in Fig. 2 are two oscillograms recorded from the healthy eye of patient G after the transient potentials induced by turning on the light had been damped. It is evident that the difference in potential $U_{an}(t)$ changes almost sinusoidally, lagging the illumination $E(t)$ by the angle δ , which increases with frequency. Similar oscillograms were obtained from more than 20 healthy eyes and from 7 eyes with a small amount of retinal pathology. The analysis showed that in the frequency range of 0.8 to 4-6 Hz (oscillograms were not made at frequencies lower than 0.8 Hz) the difference in potential $U_{an}(t)$ diverges considerably from the sinusoidal, and this is stronger the lower the frequency. Above 4-6 Hz the change in $U_{an}(t)$ was very close to sinusoidal. A change in E_m from 50 to 20 lux did not exert an appreciable effect on the shape of the curves. Thus, the operator relating the light stimulus and the ERG can, with sufficient accuracy, be considered linear and stationary in specific ranges of frequency and illumination. /34

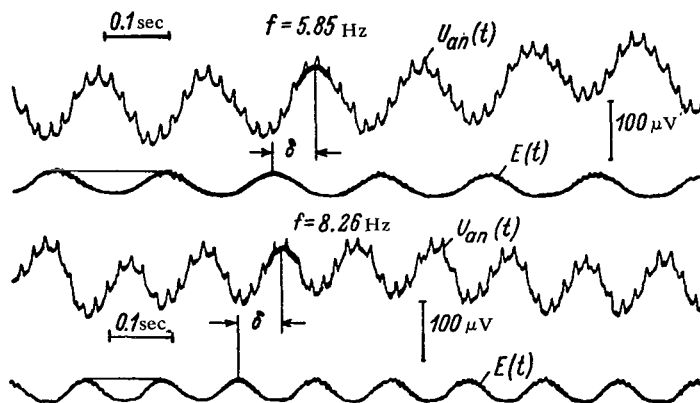


Figure 2. ERG from the Application of Sinusoidal Light Stimuli to the Eye.

Linear stationary operators characterizing the electrical activity of the retina in these ranges are completely determined by the APFC. In order to find the "sensitivity" of the frequency characteristics to pathological processes occurring in the retina and to exclude possible discrepancies between the APFC of healthy retinas, the frequency characteristics for both eyes of the same person

were compared. Of special interest were subjects with pathology localized in one eye, e.g., patient P, who arrived at the clinic with dull pain in the left eye. Upon arrival the visual acuity of the right eye was 1 and the fundus was without change; the visual acuity of the left eye was 0.02; the fundus was not examined with the ophthalmoscope. The frequency characteristics were determined after clarification of the fluids, when ophthalmoscopy revealed edema of the retina, hemorrhaging into the region of the macula lutea and around the disk of the optic nerve. Examinations with the projection perimeter and campimeter revealed central scotoma and enlargement of the blind spot.

The amplitude frequency characteristics are shown in Fig. 3; the curve a corresponds to the right eye (healthy), b to the left eye, with the pathological process. A tendency to decreasing amplitude with frequency is detected in both curves, but it is more strongly pronounced in the curve corresponding to the diseased eye. Given in Fig. 4 are the phase frequency characteristics for both eyes; they are essentially coincident. At frequencies below 4 Hz the amplitude and phase were determined from the first-harmonic difference in potential $U_{an}(t)$. /35

The APFC of the right (a) and left (b) eyes illustrated in Fig. 5 were constructed from the amplitude and phase frequency characteristics. Not directly plotted on the APFC are the amplitudes of the difference in potential $U_{an}(t)$ in microvolts, but their ratios to the value of the illumination E_m , expressed in relative units [the amplitude of the first-harmonic difference $U_{an}(t)$, which equals 100 microvolts when $E_m = 100$ lux, corresponds to the reference variable, i.e., $S(\omega)$]. The figures alongside the APFC points correspond to the frequencies of variation of the light flux. In the high-frequency range the hodograph of APFC breaks off at the critical frequency of flicker fusion (CFFF). The CFFF for the healthy right eye is 28 Hz; the CFFF was not established for the left eye, since the APFC was not determined for frequencies above 10 Hz.

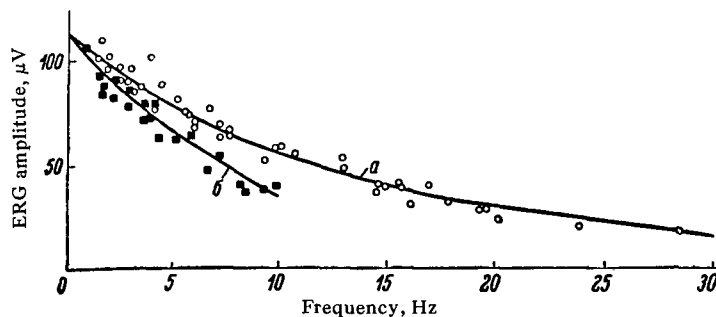


Figure 3. Amplitude Frequency Characteristics Obtained from the Right (a) and Left (b) Eyes of Patient P.

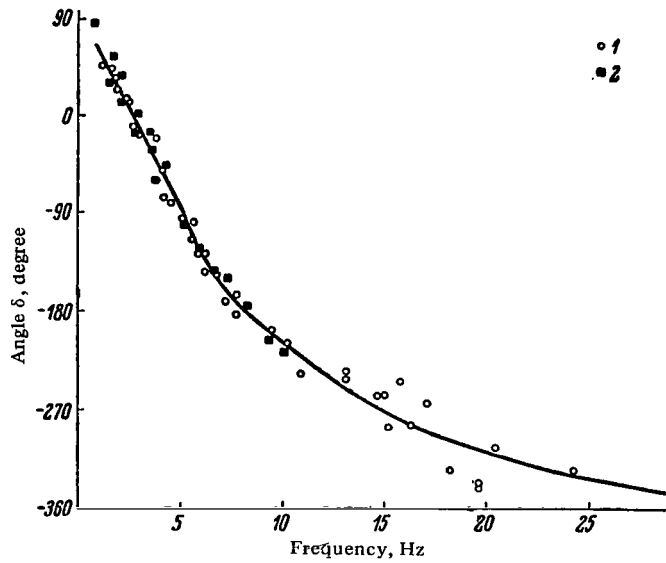


Figure 4. Phase Frequency Characteristics Obtained from Patient P. 1 - Left Eye; 2 - Right Eye.

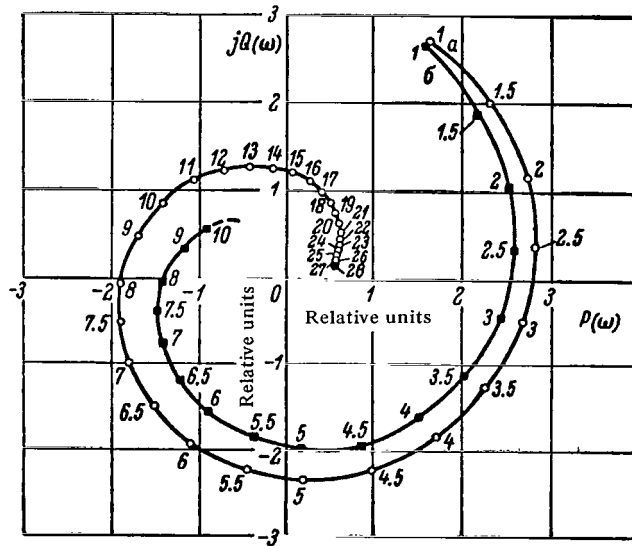


Figure 5. APFC Obtained from the Right and Left Eyes of Patient P. Symbols Explained in the Text.

Phase Determination and Wedensky's Phenomenon. In determining the phase shift between the stimulus and the evoked potential an angle error of 180° can be committed. In order to avoid this type of error, the test illustrated by the oscillogram of Fig. 6 was carried out at a number of frequencies. As is evident, termination of the application of light permits clear determination of the points on the curves $E(t)$ and $U_{an}(t)$ that correspond to each other.

/36

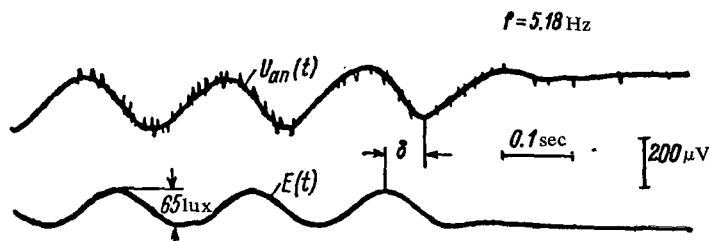


Figure 6. Oscillogram of a Test for Determination of the Angle of Shift Between the Stimulus and the Evoked Potential.

A change in the phase shift δ with frequency reveals an interesting phenomenon that seems to be paradoxical from the physical viewpoint: if the angle δ is negative at high frequencies, i.e., the difference in potential lags the illumination $E(t)$, the angle δ is positive at frequencies below 2.5 Hz, i.e., the potential reaches a maximum before the stimulus inducing it. This phenomenon is demonstrated by the oscillograms given in Fig. 7. It can be explained on the basis of the theory of parabiosis of N. E. Wedensky as developed in the studies of Semenovskaya [6], Bogoslovskiy [1], Semenovskaya and Zaretskaya [7] and Byzov [2] for the case of the visual organ. Wedensky found that upon excitation of the nerve of a neuromuscular preparation by electrical current, the strength of muscle contraction increases with increasing current intensity, but only up to a certain point, beyond which complete weakening of the muscles takes place. The oscillograms (Fig. 7) demonstrate approximately the same phenomenon, but the illumination $E(t)$ is involved instead of electrical current and the difference in potential $U_{an}(t)$ instead of muscular contraction.

/37

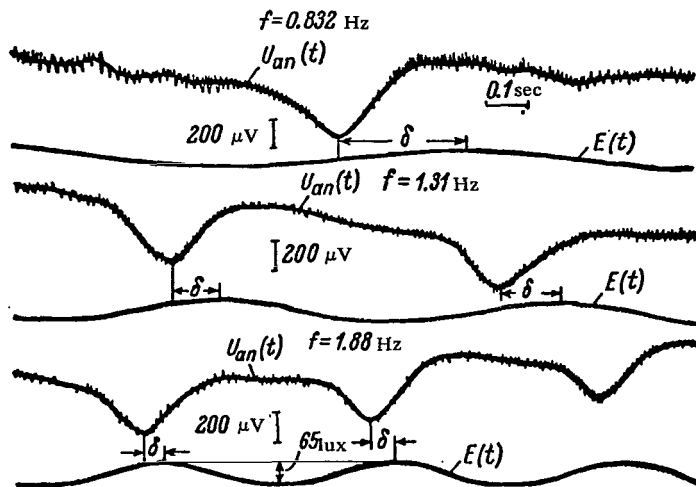


Figure 7. Response of the Retina to a Sinusoidally Varying Light Stimulus of Low Frequency, Demonstrating Wedensky's Phenomenon.

Calculation of a Transient Process from the APFC. The transient processes of a system described by a linear stationary operator can be calculated from the frequency characteristics of the system. For the case being considered, this means that the potentials evoked by stimuli of varying shape can be found from the experimentally determined APFC of the retina. Shown in Fig. 8 is the pulse response of the retina, i.e., the potential evoked by applying a stimulus in the form of a pulse function, calculated by means of numerical integration of Eq. (8). The duration of the process is 0.5 sec, since APFC points of 2 Hz and above were chosen for the calculation. /38

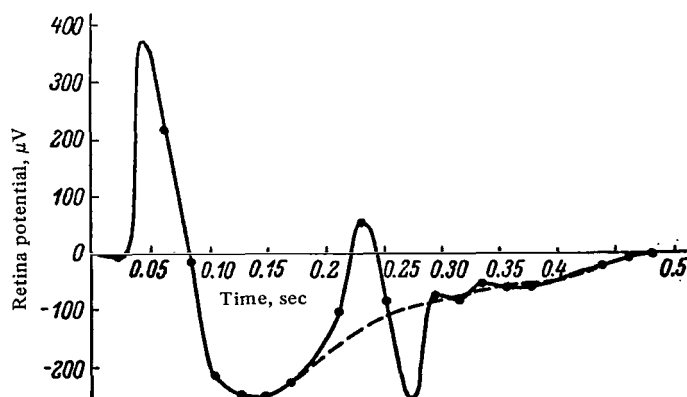


Figure 8. Pulse Response of the Retina, Calculated from the APFC.

CONCLUSIONS

1. In specific ranges of frequency and illumination of the pupil of the eye the relationship between the light stimulus and the potential evoked by it can be described by means of a linear stationary operator.
2. In order to specify the linear stationary operator, the APFC, determined experimentally, is used.
3. The study of the amplitude-and phase-frequency characteristics in various pathological processes in the retina can yield valuable data for diagnostic purposes.
4. The lag of the maximum value of a sinusoidally varying light stimulus behind the maximum of the potential evoked by it can be explained on the basis of Wedensky's principle.
5. The mathematical model describing the relationship between the stimulus and the potential by means of a linear stationary operator establishes definite relationships between the potentials evoked by light stimuli of varying shape.

REFERENCES

1. Bogoslovskiy, A.I. Problemy fiziologicheskoy optiki (Problems in Physiological Optics), 2, 136, 1944.
2. Byzov, A.L. Problemy fiziologicheskoy optiki (Problems in Physiological Optics), 12, 358, 1958.
3. Weiner, N. The Fourier Integral and Certain of its Applications, New York, Dover Publications, 1951.
4. Voronin, G.V., Sh. Tott and Ye.N. Sokolov. Biofizika (Biophysics), 9, No. 1, 94, 1964.
5. Ol'denburger, R. In the Collection Chastotnyye metody v avtomatike (Frequency Methods in Automation, Russian translation), Moscow, 1957, p. 10.
6. Semenovskaya, Ye.N. Elektrofiziologicheskiye issledovaniya v oftal'mologii (Electrophysiological Research in Ophthalmology), Medgiz, Moscow, 1963.
7. Semenovskaya, Ye.N. and R.B. Zaretskaya. Problemy fiziologicheskoy optiki (Problems in Physiological Optics), 12, 377, 1958.
8. Kharkevich, A.A. Spektry i analiz (Spectra and Analysis), Moscow, 1957.
9. Van der Tweel and P. Visser. Electroencephalographia Symposium (Electroencephalography Symposium), Zuhacovice, 1959.

Chair of Eye Diseases
Erevan Institute for the Advanced Training of Doctors



POSSIBLE FORMS OF COLOR VISION

N. V. Lobanova

The spectral sensitivities of twelve normal and deuteranomalous trichromat, as well as one protanomalous and one tritanomalous trichromat are described.

The existence of various forms of color vision has long been known, but there is as yet no consensus on the number of these forms, on the methods for recognizing them, and on their nature.

/39

Although many problems of color vision are solved by means of functions of composition of spectral properties for normal trichromats, only knowledge of the spectral sensitivity of the retinal receptors for each form of color vision will enable construction of a clear system of classifying these forms.

In collaboration with N. I. Speranskaya we determined the spectral sensitivity of retinal receptors for twelve normal trichromats, twelve deuteranomalous, one protanomalous and one tritanomalous trichromats [2, 3, 5]. The spectral sensitivity of the retinal receptors was determined by the method described by Bongard and Smirnov [1] in 1955. The results turned out to sufficiently definite for almost all the observers and for all the receptors. An exception was the third receptor of the tritanomalous trichromat, which we did not succeed in determining.

The following results were obtained.

1. The spectral-sensitivity functions of the first receptors of the normal trichromat, the deuteranomalous trichromat and the tritanomalous trichromat coincided. The spectral sensitivity of the first receptor of the protanomalous trichromat turned out to be different from the above (Figs. 1a and d).
2. The spectral-sensitivity functions of the second receptors of the normal, protanomalous and tritanomalous trichromats coincided. The spectral sensitivity of the second receptor of the deuteranomalous trichromat differed from the above (Figs. 1b and d).
3. The spectral-sensitivity functions of the third receptors of the normal, protanomalous and deuteranomalous trichromats coincided (Fig. 1c).

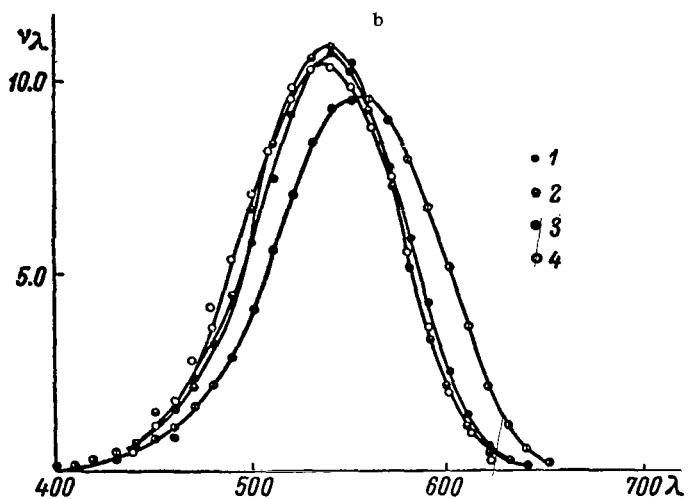
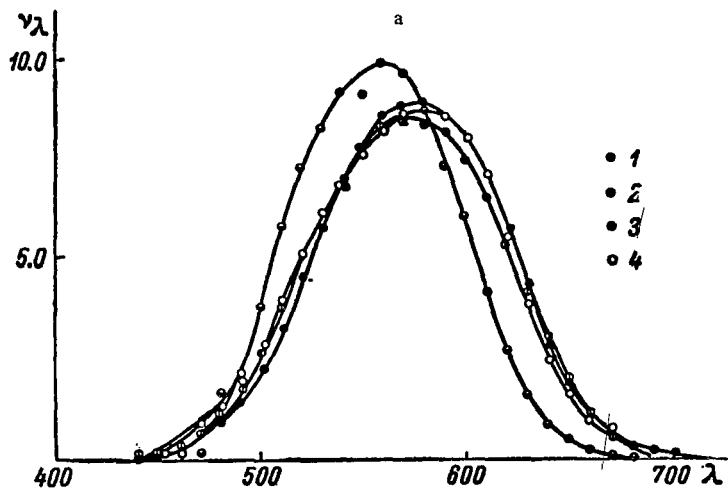


Figure 1. Spectral-sensitivity Functions of the First (a), Second (b), Third (c) and Anomalous Receptors (d).

a, b, c: 1 - Normal Trichromat; 2 - Protanoma-
lous Trichromat; 3 - Deuteranomalous Trichromat;
4 - Tritanomalous Trichromat; d: 1 - First Recep-
tor of the Protanomalous Trichromat; 2 - Second
Receptor of the Same.

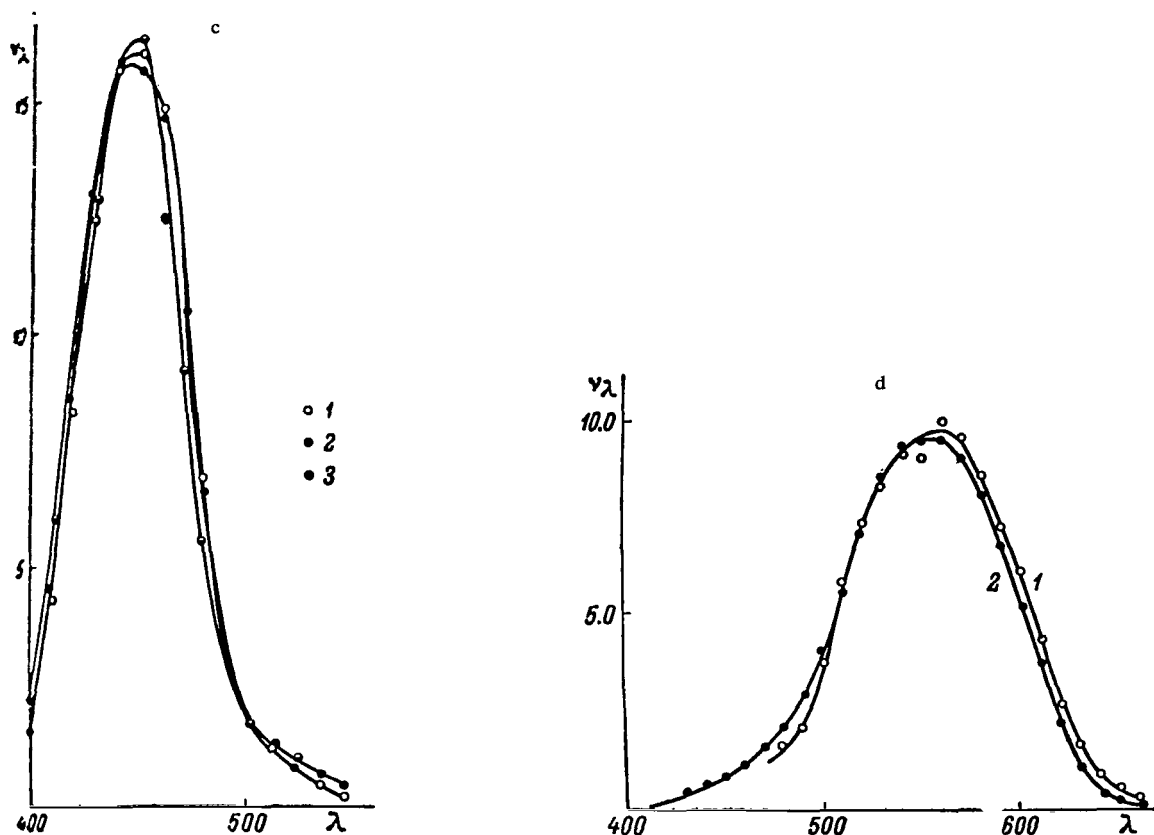


Figure 1. (Continuation)

4. The spectral-sensitivity functions of the anomalous receptors of the protanomalous and deuteranomalous trichromats coincided (Fig. 1d).

This gave us reason to assume that the spectral sensitivity of the anomalous receptor of the tritanomalous trichromat was the same as in the anomalous receptors of the protanomalous and deuteranomalous trichromats. There are indirect indications that permit us to consider this assumption to be somewhat justified [2]. We assumed that there are a total of four different types of spectral sensitivity of the retinal receptors. On the basis of this hypothesis the following schemes of possible color-vision forms can be set up.

1. Trichromatism. There are four forms of trichromatism: one normal trichromatism, for which the spectral-sensitivity functions of the retinal receptors as shown in Fig. 2a are characteristic, and three forms of anomalous tri-

/41

2. Dichromatism. There are three forms of normal dichromatism and three forms of anomalous dichromatism. The spectral-sensitivity curves for the retinal receptors shown in Figs. 2e, f, g are characteristic of each of the

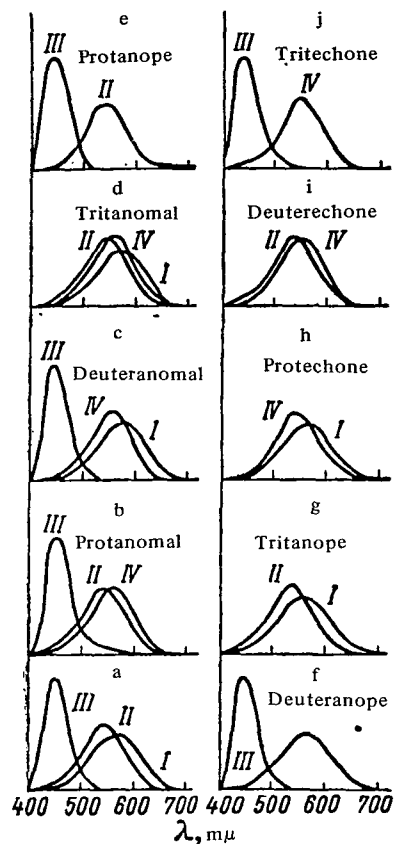


Figure 2. Possible Forms of Color Vision. Receptor Spectral-Sensitivity Functions.

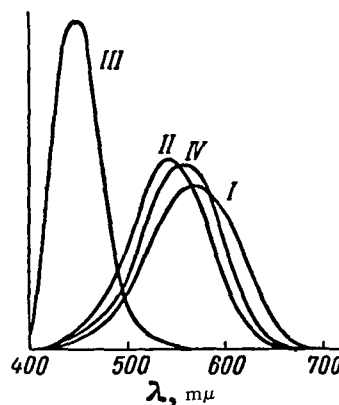


Figure 3. Tetrachromatism. Optical-Receptor Spectral-Sensitivity Curves.

three forms of normal dichromatism. Their names are protanopia, deuteranopia, and tritanopia [4]. The retinal-receptor spectral-sensitivity curves shown in Figs. 2h, i, j are characteristic of each forms of anomalous dichromatism. Names have not yet been decided upon for these forms. The following names are proposed: protechonia, deuterechonia, and tritechonia.

Ten forms of color vision are listed. It is logical to add one more form of color vision, for which the presence of all four retinal receptors is characteristic. In doing so, of course (Fig. 3), we are saying that color space is no longer three-dimensional, but four-dimensional. This form of color vision can be called tetrachromatism (Fig. 3).

The proposed scheme for the possible forms of color vision, based on the hypothesis that there are a total of four types of spectral-sensitivity functions for the retinal receptors, obviously requires verification.

/42



Form of color vision	Receptors determining the given form of color vision				No. of receptors	Persons having the given form of color vision
	I	II	III	IV		
Tetrachromatism	I	II	III	IV	4	Tetrachromats
Normal trichromatism	I	II	III	-	3	Normal trichromats
Protanomaly	I	II	III	IV	3	Protanomals
Deuteranomaly	I	-	III	IV	3	Deuteranomals
Tritanomaly	I	II	-	IV	3	Tritanomals
Protanopia	-	II	III	-	2	Protanopes
Deuteranopia	I	-	III	-	2	Deuteranopes
Tritanopia	I	II	-	-	2	Tritanopes
Protechnia	I	-	-	IV	2	Protechones
Deuterechnia	-	II	-	IV	2	Deuterechones
Tritechnia	-	-	III	IV	2	Tritechones

REFERENCES

1. Bongard, M. M. and M. S. Smirnov. Dok. AN SSSR, 102, 1111, 1955.
2. Lobanova, N. V. and N. I. Speranskaya. Biofizika (Biophysics), 6, 596, 1961.
3. Lobanova, N. V. Optika i spektroskopiya (Optics and Spectroscopy), 19, 128, 1965.
4. Lobanova, N. V. Optika i spektroskopiya (Optics and Spectroscopy), 19, 448, 1965.
5. Speranskaya, N. I. and N. V. Lobanova. Biofizika (Biophysics), 6, 472, 1961.

State Optical Institute
Leningrad

Ye. B. Rabkin

The author plots schematic curves of saturation, visibility, electrical sensitivity, adisparopia, functional stability and color fatigue in the spectrum of normal trichromats. The indicated regularities in the features of the medium-wave portions of the spectrum and the reactions of the optical analyzer in the process of adaptation to them serve as a basis for our setup of the spectral equation.

In expanding Maxwell's thesis as to the possibility of getting yellow from a mixture of red and green, Rayleigh [5] proposed a color equation based on the law of color mixing. This equation was used subsequently in the form of a spectral equation consisting of the following: it is possible to get two color fields defined by Rayleigh's equation using a device called an anomaloscope. One of these fields is formed by the monochromatic orange-yellow color of the Na line, $\lambda = 589 \text{ m}\mu$, the other field of the same color is obtained by mixing the red color of the Li line, $\lambda = 671 \text{ m}\mu$ with the green color of the He line, $\lambda = 535 \text{ m}\mu$.

The color equation was found, at a later date, to be applicable in scientific studies of color vision and in diagnosis of congenital forms of color-vision disturbances. It should be emphasized that complete identity between monochromatic color and color obtained from the mixing of two monochromatic colors can be achieved only by balancing out the brightness of the two fields of the anomaloscope.

From separate disconnected facts and different interpretations of the phenomena of color derangements concepts of these derangements and their classification were gradually developed. Thus, Kries [3] published a classification of color-vision disturbances proposed by him. But not all the forms of color pathology fit within the framework of Kries' classification. According to the data of several authors, in most cases color disturbances differ in their characteristic features from dichromatic forms of disturbances and also from the acquired pathology of color vision.

Owing to the fortunate hypothesis of the existence of a special, anomalous-trichromatic form of color disturbance, which was subsequently advanced by Nagel using the spectral Rayleigh equation, Kries' classification was supplemented by



two forms of anomalous trichromatism called protanomaly and deuteranomaly by Nagel. The classification of Kries and Nagel, with some corrections, is considered to be the best-founded even at the present time.

Later on Rabkin [2] also supplemented it with three types (degrees) of color disturbances A, B and C, where A refers to the most sharply pronounced degrees of protanomaly and deuteranomaly, B refers to moderate cases and C to slight cases.

The basic prerequisite for Nagel's use of Rayleigh's equation to differentiate between protanomaly and deuteranomaly was the establishment of the following characteristic: in the spectral field of the device that includes two mixed monochromatic colors anomalous trichromats perceive not the resultant orange-yellow color, but only one of the monochromatic exciters. Thus, protanomals, correctly perceiving the monochromatic orange-yellow color, take the same color formed by mixing of the two monochromatic colors red and green as green, since their sensation of red in the mixed red-green color is reduced. Deuteranomals, on the other hand, take the mixed red-green color as red, since their sensation of green is reduced.

/44

Thus, according to Nagel's assertion, neither protanomals nor deuteranomals accept Rayleigh's equation, which distinguishes them from the dichromats, namely, the protanopes and deuteranopes. It should be noted, however, that some well-known corrections were subsequently introduced into this thesis. They reduce essentially to the fact that protanomals and deuteranomals of only the slight and moderate degrees (types C and B) do not accept Rayleigh's equation, while extremanomals (extreme anomals), or anomalous type-A trichromats in our classification of degrees of color-vision disturbance, accept this equation, as do dichromats.

The use of Rayleigh's equation proved to be highly valuable in scientific studies of congenital color-vision disturbances, and also in clinical practice. The latter is connected primarily with the fact that the anomalous trichromats, the protanomals and deuteranomals, make up about 70% of patients with congenital color-vision disturbances, according to the data of various authors and of a large number of studies in our color-vision laboratory.

The tremendous amount of material that has accumulated over the world on clinical-diagnostic studies of color vision, particularly the thirty years of laboratory experience (more than 40,000 normal trichromats, anomalous trichromats and dichromats) shows that the most exact determination of the forms and degrees of congenital color disturbance is achieved by the spectral equation method, and also by color tables, which, in their diagnostic properties, approximate the spectral devices, thus ensuring differential diagnosis of congenital color-vision disturbances. Thus, the spectral equation method, as a research principle, has permanently entered the arsenal of physiological and clinical color-vision research under normal and pathological conditions. It is not accidental, therefore, that the classical spectral equation of Rayleigh has been used for about 60 years.

At the same time, however, the use of the Rayleigh equation runs up against some well known difficulties in a number of cases, at least according to the literature data, as well as the research data of the color-vision laboratory of VNIIZhT*. These difficulties revolve around the fact that in the process of exposing some anomalous trichromats to the Rayleigh equation, uncertainty arises in evaluating it. In practice, this means that after the Rayleigh equation is accepted, it is later rejected, and vice versa.

A large number of authors, in particular Trendelenburg [6] and others, have established that in the process of observing color fields many subjects have the sensation of color fatigue, of color asthenopia (according to Engelking) or color adisparopia (according to Rabkin). In the state of adisparopia, albeit temporary, the subjects often accept equations which are not adequate to their type of color vision, and as a result diagnostic errors are inevitable. Thus, e.g., anomalous trichromats of the moderate and slight degrees of the deuteranomaly type, and especially of the protanomaly type, accept the Rayleigh equation if there is no limitation on their time of adaptation.

This phenomenon can be explained by the fact that the change in perception of the orange-yellow field consisting of extreme red mixed with green takes place during adaptation considerably faster under the influence of adisparopia than in the case of adaptation to the same orange-yellow monochromatic color. For this reason, Trendelenburg and others consider as actually accepted only those relations between the original colors of the mixture to which the subjects adapt in no more than three seconds. But such a short period of adaptation to color exciters, especially those of the extreme ends of the spectrum, does not always guarantee adequate response to color.

/45

The above-mentioned phenomena of temporal reduction in color perception and uncertainty and contradiction in responses upon observation of the Rayleigh equation are associated primarily with the fact that this equation includes the monochromatic red color of the lithium line, which by its very nature is highly saturated.

It has been shown experimentally that colors of the extreme ends of the spectrum have the greatest saturation [4, 1]. In this context, color fatigue, decelerating processes, reduction in functional stability of chromatic vision, adisparopia, transient decrease in the color-discrimination function and other phenomena occur during the process of adaptation to such zones. Within the framework of further development of the spectral equation method and of its introduction into clinical and physiological practice, the problem of the construction of spectral equations from stimuli of other portions of the spectrum, less fatiguing ones, ones which reduce the functional stability of chromatic vision to a lesser degree and ones which vary less in the perception of observers subjected to adisparopia during adaptation, has been studied for a number of years in the color-vision laboratory of VNIIZhT.

* VNIIZhT = All-Union Scientific Research Inst. for RR Transportation.

As the theoretical basis for the establishment of an optimal spectral equation, with allowance for the physiological features of the optical analyzer, we took the already-determined laws of distribution of saturation and relative spectral visibility as well as the various manifestations of adisparopia, color fatigue and functional stability of chromatic vision as a function of the wavelength of the compared radiation.

The maximum of the spectral sensitivity of the average human eye is found to lie, as is well known, in the yellow-green zone $\lambda = 556 \text{ m}\mu$.

Our experiments showed that the maximum stability of color discrimination and the time thresholds of adisparopia in persons with normally trichromatic vision fall in the zone of maximum sensitivity of the average human eye. At the same time, however, the levels of saturation and of color fatigue in this central zone of the spectrum are very low. Such relative coincidence between the basic curves is apparently not accidental, but is contingent on the amazing capacity of the human visual organ to perceive solar radiation, which has been generated in the process of man's long evolution, in the process of phylogenesis and ontogenesis.

/46

Shown in Fig. 1 are schematic curves of saturation, visibility, electrical sensitivity, adisparopia, functional stability and color fatigue in the spectrum of normal trichromats. The indicated regularities in the features of the medium-wave portions of the spectrum and the reactions of the optical analyzer in the process of adaptation to them served as a basis for our setup of the spectral equation. The equation was worked out by us as a result of our experimental research and clinical tests. It consists of the monochromatic yellow-green color of the Mg line with a wavelength of $\lambda = 570 \text{ m}\mu$ for one half of the spectral field and of two monochromatic colors, red of the Cu line with a wavelength of $\lambda = 640 \text{ m}\mu$ and green of the Hg line with $\lambda = 521 \text{ m}\mu$, for the other half of the field. The resultant color from the mixing of the last two exciters is adequate for the perception by normal trichromats of the above-cited yellow-green color (Fig. 2).

These regularities characterize the spectral equation as being physiologically optimal for differential diagnostics of congenital color-vision anomalies.

A construction of the spectral equation on the spectroanomaloscope (Fig. 3) is carried out as follows:

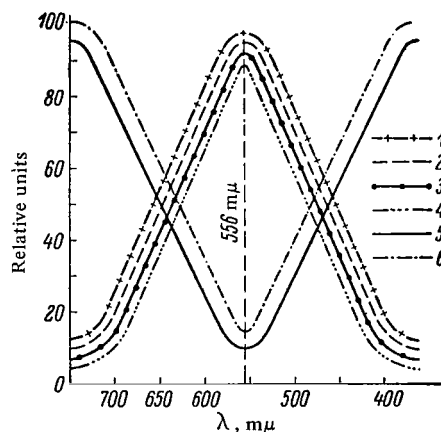


Figure 1. Schematic Curves of Visibility 1 - Stability, 2 - Adisparopia, 3 - Electrical Sensitivity, 4 - Saturation, 5 - Color Fatigue, 6 - In the Spectrum.

Plotted on the Abscissa is the Wavelength in $\text{m}\mu$ and on the Ordinate the Sensitivity to Monochromatic Light (ν_λ).

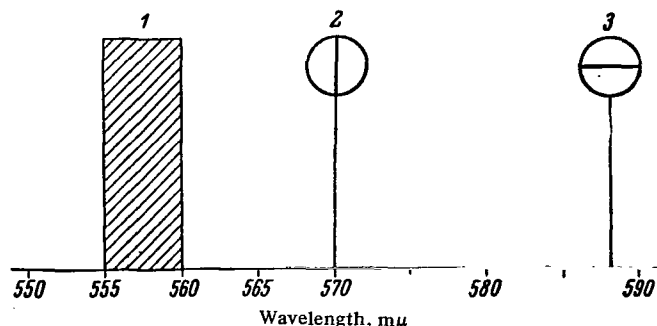


Figure 2. Schematic Arrangement of the Values of the Spectral Equations Relative to the Zone of Maximum Sensitivity of the Eye: 1 - Zone of Maximum Sensitivity; 2 - Rabkin's Equation; 3 - Rayleigh's Equation.

the left-hand measuring drum (from the observer's viewpoint) is set at the red mark, $\lambda = 640 \text{ m}\mu$ (by the red scale) and $\lambda = 521 \text{ m}\mu$ on the black mark (by the black scale). By pointing the dial on the left handle upward, both slots for transmission of the two above mentioned colors are opened for mixing. The left knob with the measurement scale that indicates the relationship between the two monochromatic stimuli when they are being mixed is set at 25. The right measuring drum is set on the red mark, $\lambda = 570 \text{ m}\mu$. Pointing the dial on the right handle away from the observer opens the slot that transmits only one monochromatic color. The right knob with the measuring scale is set at 49. It should be kept in mind that the values on the scales of the two knobs can vary in the range ± 2 divisions at the level of instrumental spectral-field brightness generated by the light source within the instrument. With another light source the values may vary over a broader range.

/47

On the basis of data from the examination of many subjects with normal and anomalous color vision, S. Ya. Freyman and A. A. Mitnik determined the value on the measurement scale of the left knob that characterizes the color shade of the right half of the spectral field and also the value on the measurement scale of the right knob that characterizes the brightness of the left half of the spectral field.

It should also be pointed out that it is necessary to try to achieve constant light-source radiation during the experiment in order to ensure that the indices on the measurement scale of the instrument are of the same value.

The spectral equation we have proposed can be used both for experimental physiological and clinical studies of color vision in normal and pathological cases. The spectral equation can be displayed on the ASR spectroanomaloscope of our system (Fig. 3), on a Helmholtz spectral apparatus for color mixing and by means of other devices that permit operation with radiations of the entire visible spectrum.

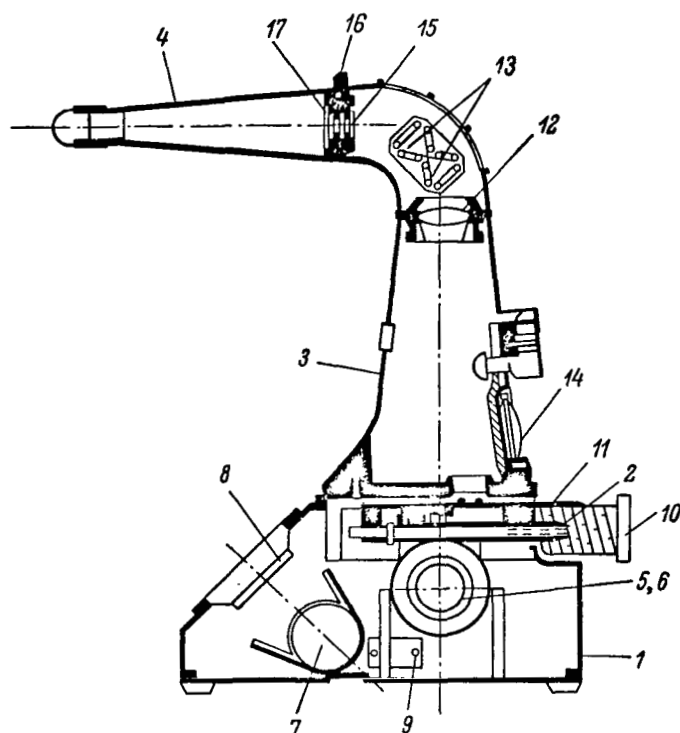


Figure 3. Cutaway Diagram of the ASR Spectro-anomaloscope: 1 - Housing with Illuminator; 2 - Slot Mechanism; 3 - Tube with Objective and Spectral Prisms; 4 - Observation Tube; 5, 6 - Electric Lamps; 7 - Bulb for Illumination of the Adaptor; 8 - Adaptor; 9 - Commutator; 10 - Drum and Scales with Wave Indicators; 11 - Dial; 12 - Collimator Objective; 13 - Spectral Prisms; 14 - Stop Watch; 15 - Biprisms; 16 - Disk and Diaphragm; 17 - Objective.

REFERENCES

/48

1. Kravkov, S. V. Tsvetovoye zreniye (Color Vision), Moscow, 1952.
2. Rabkin, Ye. B. Vestnik oftal'mologii (Journal of Ophthalmology), 17, 5, 1940.
3. Kries, G. Ueber Farbensysteme (On Color Systems), Z. f. Psych. u. Physiol. der Sinnesorgane (Journal of Psychology and Physiology of the Sensory System), 13, 1897.
4. Martin, L. Report of a Joint Discussion of Vision, Cambridge, 1932.
5. Rayleigh, O. M. Nature, 25, 64, 1881.
6. Trendelenburg, W. Klin. Monatsberichte f. Augenheilkunde, 83, 21, 1929.

Color Vision Laboratory
VNIIZhT

LIGHT AND COLOR THRESHOLDS OF LIGHTS AGAINST A BACKGROUND OF DIFFERENT BRIGHTNESS

/49

R. L. Fol'b and S. V. Voronina

The data obtained by the authors make it possible to calculate the intensity of constant and flashing colored signal lights used at night against a background of low brightness.

The level of visual perception of a constant light is determined by the illumination, by the luminescence on the pupil of the observer's eye. The threshold value of the luminescence depends on the brightness of the background against which the light is seen, on the position of the retina by which the observer fixes it, and on the time of observation. The lower the brightness against which the light is seen, the lower the threshold luminescence. The level of visual perception of the flashing light together with the amount of illumination (the product of the luminescence and the duration of the flash) can also be governed by the duration of the flash, by its period and by the shape of the light pulse.

Many authors have studied the light threshold of lights, both in the laboratory and in the field. A list of the papers written on the study of the light threshold prior to 1933 is given in the article by Vishnevskiy and Tsyrlin [3], from which it follows that the experimental conditions exert a considerable influence on the results obtained. The dependence of the threshold luminescence on the brightness of the background and on the degree of peripheral observation of the signal light was obtained by Pinegin and Travnikova [6].

In threshold detection of lights the observer cannot recognize the color of the light. In order to distinguish the color the luminescence must be above-threshold. The luminescence corresponding to the level of color recognition is called the threshold of color sensation, in contrast with the light threshold, which is sometimes called the colorless or achromatic threshold. In order to distinguish the color of a light, its image must strike the pupil in a zone with angular dimensions of $\pm 15^\circ$ from the center of the fovea [7]. If the image of the light strikes the periphery of the retina, the light is perceived as colorless. The color-sensation threshold depends on the color of the light and on the brightness of the background against which it is observed. Hartridge's study [16] shows that when the angular size of the light changes from 7' to 8", the color perception changes. Thus, blue monochromatic radiation at 7' ($\lambda = 460 \text{ m}\mu$) becomes pale greenish blue at 41", dark gray at 20" and colorless at 8"; red monochromatic

radiation ($\lambda = 720 \text{ m}\mu$) becomes amber at 41", dark brown at 20" and light brown at 8".

Rautian and Speranskaya [7] have made an analysis of the experimental results of different authors on the recognition of color published prior to 1948; on the basis of this analysis they standardized the values of color-sensation threshold.

In studying color-sensation thresholds for the purpose of making colored lights, individual researchers use either colored light filters with a broad passband [4] or monochromatic radiation [16, 13, 5, 11]. In these studies the color-sensation threshold is determined with a varying degree of probability, 50, 60, 75 or 100%. As a result there is considerable discrepancy between the values of the color-sensation thresholds. /50

The ratio of the color-sensation threshold to the light threshold (achromatic) is called the achromatic (sometimes the photochromatic) interval (K). For many years it had been assumed that the achromatic interval was not greater than 10. Demkina's study [5] was the exception. For practical purposes, however, low values of the achromatic interval (1, 2, 3) continued to be used. Only in recent years has it been accepted that the achromatic interval is appreciably greater than indicated. Thus, Le Grand [15] found that the achromatic interval for radiation at a wavelength less than 550 m μ exceeds 100.

Given below are the values of the achromatic interval (K) recommended in the German Democratic Republic for red, green and yellow lights observed against backgrounds of differing brightness (B_{Φ} , nit) [14]:

B_{Φ} , nit	K
10^3 to 10^{-2}	≤ 10
10^{-2} to 10^{-4}	10 to 110

From what has been said it is evident that the achromatic interval reaches 100 for $B_{\Phi} = 10^{-4}$ to 10^{-2} and decreases with increasing background brightness. From Volinskiy's study [18] it also follows that for lights of any chromaticity the achromatic interval is observed to decrease with increasing background brightness.

Crozier has shown that curves of the luminescence-dependence of the probability of detection of a light have a different slope for different wavelengths [12]. Consequently, the shape of the curves of the wavelength-dependence of the light threshold changes with a change in the level of probability of light detection. Dagher, Cruz and Plaza also pointed out an analogous effect for the color-sensation threshold [13].

Figure 1 presents the results of measurement of the achromatic interval by Dagher, Cruz and Plaza, as averaged by us for three observers. The curves of the wavelength-dependence of the achromatic interval [$K = f(\lambda)$] for a probability of 100 and 500 % differ strongly from each other. Given also in Fig. 1 for comparison are the curves of the achromatic intervals of Demkina for the same wavelengths [5].

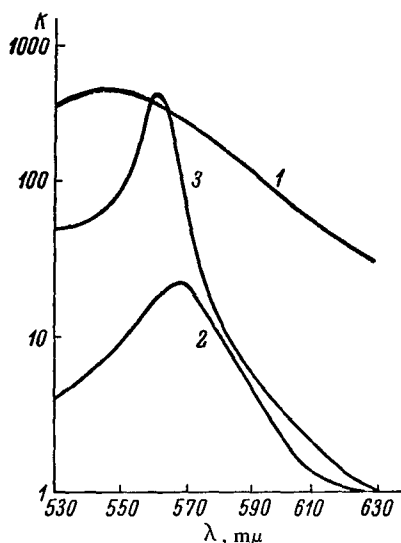


Figure 1. Spectral Dependence of the Achromatic Interval.

Plotted on the Abscissa is the Wavelength ($m\mu$) and on the Ordinate is the Achromatic Interval ($K = \frac{\text{Color Sensation Threshold}}{\text{Light Threshold}}$): 1 - the Data of Dagher, Cruz and Plaza for $P = 100\%$; 2 - the Same for $P = 50\%$; 3 - the Data of Demkina for $P = 50\%$.

TABLE 1. Experimental Conditions, Data of Various Authors (Fig. 1).

/51

Author	Angular size of light (min)	Probability of color recognition (%)	No. of observers	Time of display of the light (sec)	Range of measurement of the chromaticity of the light ($m\mu$)
Dagher, Cruz and Plaza [13]	15	50	3	3, with an interval	from 530-630 two observers
Dagher, Cruz and Plaza [13]	15	100	3	"	"
Demkina [5]	1	50	10	Unlimited	from 430 to 680 10 observers

Given in Table 1 are the experimental conditions of these authors. An analysis of Fig. 1 and Table 1 shows that there is a systematic dependence of the achromatic interval on the probability of recognizing the color of the light, despite the different times of presenting the light.

Thus, the values of the achromatic interval depend on the probability with which the light threshold and the color-sensation threshold are determined.

The aim of our experimental work was to determine the light thresholds and the color-sensation thresholds of flashing and also constant signal lights against a background of different brightness and to compute the achromatic interval for these conditions of observation. We made measurements of the achromatic interval of constant lights so as to obtain comparative data for flashing and constant lights under constant conditions of observation. In the experiments we used the previously described method and setup [10]. The measurements were made for four colors, namely, yellow, green, blue and red.

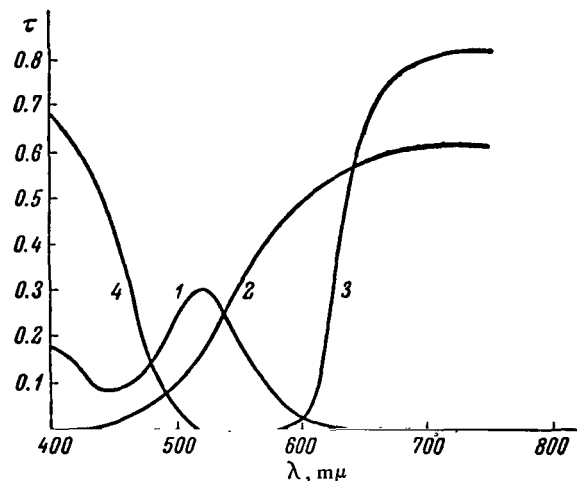


Figure 2. Spectral Transmission Curves of the Light Filters.

Plotted on the Abscissa is the Wavelength ($m\mu$) and on the Ordinate the Transmission Factor of the Light Filters (τ). 1 - Green; 2 - Yellow; 3 - Red; 4 - Green.

In order to make the colored lights we used aviation signal light filters. The spectral curves of the passband of the light filters are given in Fig. 2. The chromaticity of the incandescent-bulb radiation passing through the light filters is characterized by the coordinates given in Table 2, in which the transmission factor τ of the light filters for source A is also given.

TABLE 2. Coordinates of the Chromaticity x and y of the Lights and the Color Shade of Radiation λ for the Source A.

Light	x	y	$\lambda, m\mu$	$\tau, \%$
Red	0.692	0.308	621	13.4
Yellow	0.565	0.421	590	10.4
Green	0.233	0.550	522	38.0
Blue.	0.432	0.0410	450	1.22

The lights were observed binocularly without a fixation point against backgrounds of brightness 10^{-6} nit, 1.5×10^{-3} nit and 0.5 nit. The observer adapted to the background brightness at which he was exposed to the light. With a dark background the adaptation time was 40 min, and with the lightest background it was 20 min. With flashing lights the measurements were made at three periods of 0.4, 0.8 and 3.2 sec. The duration of the flash was 0.01 sec. The distance between the observer and the light was 2 min. The light was visible at an angle of $\alpha = 1'$. The search for the light against a 10^6 nit background was made at

an angle of $150 \times 150^\circ$, and against 1.5×10^{-3} and 0.5 nit backgrounds the search was made in the central portion of the field $30 \times 30^\circ$. During the experiments the intensity of the light was increased until the observer recognized the color of the light without error. The probability of determining the thresholds is close to 100%.

TABLE 3. Mean Values of the Light Threshold (LT) and Color-Sensation Threshold (CT) of a Constant Light, $E = 10^{-9}$ lux, and a Flashing Light, $E t = 10^{-9}$ lux sec.

Type of light	Color of light	B_ϕ , nit $\times 10^{-6}$			B_ϕ , nit 1.5×10^{-6}			B_ϕ , nit $\times 0.5$		
		LT	CT	K	LT	CT	K	LT	CT	K
Constant	yellow	4	350	90	80	540	8.5	260	1560	6.0
	green	2.5	320	120	70	400	6.0	400	900	2.5
	red	21.0	23	1.1	80	80	1.0	200	200	1.0
	blue	0.45	550	1200	25	1480	60	300	1000	3.5
Flashing ($t = 3.2$ sec)	yellow	6.0	400	60	18	150	8.4	26	100	4.0
	green	3.6	380	100	16	240	15	32	120	3.5
	red	19	20	1.1	18	18	1.0	30	30	1.0
	blue	0.5	120	240	10	150	15	-	-	-
Flashing ($t = 0.8$ sec)	yellow	4.1	80	18	17	98	8.0	27	120	4.5
	green	2.8	400	140	11	280	20	28	120	4.0
	red	11	12	1.1	13	13	13	18	18	1.0
	blue	0.8	200	250	20	250	20	10	-	-
Flashing ($t = 0.4$ sec)	yellow	3.7	250	15	13	100	7.0	30	140	4.7
	green	1.4	200	150	10	220	23	25	100	4.0
	red	10	11	1.1	11	11	1	12	12	1.0
	blue	0.5	250	500	7	290	40	10	-	-

Given in Table 3 are the average (for 7 observers) values of the light thresholds and color-sensation thresholds for constant and flashing lights, as well as the calculated values of the achromatic interval for yellow, green, red and blue; these were obtained by dividing the corresponding values of the color-sensation threshold by the light threshold for each observer and then averaging.

The achromatic interval for the red light during observation against a 10^{-6} nit background was usually 1. There were cases, however, when red was recognized only after continued observation of the light; this can probably be explained by the fact that the light was first fixed by the periphery of the retina. For this level of background brightness the achromatic interval of the red signal was taken equal to 1.1. At higher levels of brightness the achromatic interval for the red light was always 1. For the constant blue light against a 10^{-6} nit background the values of the achromatic interval reach 1,000 and above.

As is evident from Table 3 the achromatic interval decreases for all colors /53 with increasing background brightness.

The data we obtained on the achromatic interval for constant lights are in good agreement with the literature data [5, 11, 13, 15].

At the same time, our experiments show that the achromatic interval for flashing lights differs from that for constant lights.

Of great practical interest is the improvement in the ability to discern blue and yellow signals (lowest achromatic interval) for flashing lights of all periods compared with the constant lights during observation against dark backgrounds (10^{-6} and 1.5×10^{-3} nit).

The data we obtained make it possible to calculate the intensity of constant and flashing colored signal lights used at night against a background of low brightness.

In order to get the color-sensation threshold of constant lights, the value of the light threshold must be increased by a factor of 1,200 for blue light, by a factor of 120 for green light, and by a factor of 90 for yellow light. Flashing blue and yellow signal lights are more effective, since a smaller increase in the light threshold is required for recognition of the color than in the case of constant lights.

REFERENCES

1. Butylev, A.A. and O.D. Barteneva. Trudy glavnoy geofizicheskoy observatorii imeni A.I. Voyeykova (Transactions of the A.I. Voyeykov Main Geophysical Observatory) 80, 39, 1959.
2. Butylev, A.A. and O.D. Barteneva. Svetotekhnika, No. 8, 25, 1957.
3. Vishnevskiy, N.A. and B.A. Tsyrlin. Svetotekhnika, No. 6, 7, 1934.
4. Vishnevskiy, N.A. and B.A. Tsyrlin. Trudy IAM VVS imeni Pavlova (Transactions of the Pavlov Air Force Aircraft Motor Construction Inst.) 1, 69, 1939.
5. Demkina, L.I. Trudy 1-oy konferentsii po fiziologicheskoy optike (Proceedings of the First Conf. in Physiol. Optics) 37, 3, 1936.
6. Pinegin, N.I. and N.P. Travnikova. Dokl. Akad. Nauk SSSR, 148, 6, 1403, 1963.
7. Rautian, G.N. and N.I. Speranskaya. Trudy GOI (Transactions of the State Optical Inst.) 24, 144, Oborongiz, Leningrad, 1955.
8. Sokolov, M.V. Problemy fiziologicheskoy optiki (Problems in Physiol. Optics) 4, 146, 1948.
9. Tekhnicheskaya instruktsiya po soderzhaniyu sudokhodnoy obstanovki na vnutrennikh vodnykh putyakh (Technical Instructions for the Maintenance of Ship Navigation on Internal Waterways), River Transportation Publ. House, Moscow, 1962.
10. Fol'b, R.L. and E.A. Belkina. Svetotekhnika, No. 9, 20, 1965.
11. Bauman, M.A. and P.L. Walraven. Visual Probl. of Colour, 1, 461, 1958.

12. Crozier, W.I. J. Gen. Physiol., 34, 5, 87, 1950.
13. Dagher, M., A. Cruz and L. Plaza. Visual Probl. of Colour, 1, 387, 1958.
14. DIN 5037, Sheet 2, June, 1963.
15. LeGrand, Y. Light, Colour and Vision, Chapman and Hall, London, 1937.
16. Hartridge, H. Phil. Trans. Roy. Soc., 232, Ser. B, No. 592, 529, 1947.
17. Hill, N. Proc. Phys. Soc. (London), 59, Part IV, 560, 1947.
18. Wolinski, L. Optik, 7, 469, 1965.

All-Union Scientific Research
Institute of Light Engineering

COLOR DISCRIMINATION IN PERSONS WITH LOW VISUAL ACUITY

A.I. Kaplan

Color discrimination was investigated in 230 children of school and preschool age with visual acuity either below 0.05 or equivalent to light perception only. Contrary to some data in the literature, normal color discrimination was found in children with a visual acuity below 0.05. In some subjects, different types of pathology of color discrimination were observed. Ye. B. Rabkin's charts can be used if the visual acuity is below 0.02.

Color vision, one of the most important aspects of the reflection and recognition of the outside world, is a highly complex visual function. Whereas the determination of photic sensitivity requires the study of only one parameter (luminance), investigation of color discrimination requires the consideration of three components: hue, saturation, and luminance. The mechanism of discrimination and perception of color has not yet received adequate study.

/54

The ability of persons with reduced visual acuity to discriminate color likewise has been inadequately studied, despite its great practical importance in the education of the blind and in their subsequent work performance. In some investigations devoted to the compensation of blindness and teaching blind children with realistic three-dimensional drawings (1) has shown that children with residual vision and sometimes even children unable to recognize the shape of an object have the emotional experience of color and can discriminate to some extent between colors. However, the limits, character, and distinctive features of color discrimination in persons with residual vision have never been studied. Under clinical conditions, color discrimination is usually not tested in children whose visual acuity is below 0.05.

Since the majority of a group of persons with residual vision studied by the writer have congenital developmental abnormalities of the organ of vision, it was decided to investigate the question of inborn color pathology in various disturbances of central vision. Congenital abnormalities of color vision were, of course, first described at the end of the 18th century [6, 8, 4]. Subsequently, many genealogies were collected, and they indicated a recessive, sex-linked type of inheritance of abnormalities of color vision.

Statistics for recessively transmitted congenital color blindness expected and actually observed, given by various writers after examination of large numbers of people, show good agreement [9, 7].

In connection with the development of genetics and investigations of color vision such chromosomal abnormalities as the syndromes of Klinefelter and Turner, new data of essential importance to the study of the pathogenesis of congenital color blindness were obtained. For example, investigation of color vision in 24 men with Klinefelter's syndrome and with an "XX" chromosome, i.e., who were "genetically women," demonstrated normal trichromasia, whereas for this number of ordinary males, two would be expected to be color blind. At the same time, of 26 men with Klinefelter's syndrome and possessing an "XX" chromosome, i.e., "genetically men," color blindness was found in four cases [10]. It will be noted that, in the light of subsequent advances in genetics, these descriptions of "genetic women" and "genetic men" must now obviously be applied to the chromosome-positive Klinefelter's syndrome in the first case, and the chromosome-negative Klinefelter's syndrome in the second case.

/55

In women with Turner's syndrome, in the absence of a second-X-chromosome, color blindness was found in 4 of 25 cases [11], i.e., the same as in the chromosome-negative Klinefelter's syndrome. On this basis the hypothesis was put forward that the incidence of congenital color blindness does not correlate with the male or female phenotype, but with the genetic sex [11].

The writer's investigations of color discrimination in Klinefelter's and Turner's syndromes, as in all other cases, were carried out by the pigment method using Ye. B. Rabkin's ASR spectral anomaloscope. Sex chromatin was investigated by M. M. Rayskaya. It was noted in particular that in some cases, even with normal trichromasia, disturbances of color vision were present.

For example, in the case of Nikolai V., born in 1950, with Klinefelter's syndrome and a 47-chromosome karyotype with sex formula XXY (acuity of central vision 0.1 in the right eye, 1.0 in the left; nystagmus of both eyes), and with normal trichromasia, a decrease in color sensitivity to red, green, and blue was observed, as shown by elevation of the color thresholds. Contrast or discriminative sensitivity also was sharply reduced. The right eye complementarily receives three equations for red, yellow, green, and blue colors. The left eye complementarily receives four equations for red and blue, five for yellow, and six for green. The functional stability of color vision is reduced. The different color equations are received for 6-10 sec.

This and similar observations indicate that when children with these syndromes are tested, it is not sufficient simply to establish their color discrimination, but it is also essential to study their color sensitivity, their contrast sensitivity, and the functional stability of their color vision, or adysparopia. This problem is being studied at the present time.

Turning to the question of color discrimination in residual vision, the writer has discovered in the literature indications of two forms of pathology of color vision: 1) congenital complete and 2) congenital incomplete achromatopsia with amblyopia [5], observed in persons with an acuity of central vision of 0.1 or a little less. The description of different disorders of color discrimination in persons with acquired disturbances of color vision, the main characteristics and methods of investigation of which have been developed in considerable detail by Rabkin [3], Kravkov [2], Segal [12] and others, do not mention the specific features of color discrimination in persons with residual vision. The writer has studied color discrimination in 230 children of preschool and school age with such severe disturbances of shape perception that they are categorized as blind. The severe disturbances of vision were the result of various pathological processes, 64.9 % being congenital and 25.4% acquired, while 3.7% of the lesions of the organ of vision were associated with conditions arising during childbirth so that in individual cases it was difficult to exclude the existence of antenatal factors. In 6% of cases the nature of the pathological process ending in blindness was unknown.

A study of the primary anatomical localization of the pathological process indicated a lesion of the visual system as a whole or of its various components: the media of the eye, retinal receptors, the channel of transmission (most frequently), and the higher visual centers. The investigations showed that in the presence of severe lesions of the media of the eye, mainly in congenital cataract and aphakia, after its removal, in most cases normal trichromasia was discovered, including cases when the acuity of central vision was below 0.01. Some ability to discriminate color remained even in the absence of discrimination of shape.

/56

A fact of particular significance was that, in lesions of the neurovisual system of the organ of vision with a similar clinical picture, different types of pathology of color discrimination were found in the subjects. In some cases the results of color discrimination tests were used to assess the severity of the lesion of the visual functional system, to ascertain the state of its individual components, and for the purpose of differential diagnosis.

This investigation shows that, although color discrimination is a highly differentiated, delicate, and complex function, and is extremely unstable, yet the ability to distinguish color can persist for a long time, just as is the case with light perception, despite severe and lasting lesions of the visual system. This may provide some opportunities for the use of color discrimination by virtually blind people in their activities and also for the study of many problems connected with color discrimination.

REFERENCES

1. Zemtsova, M.I. Puti kompensatsii slepoty (Ways of Compensation for Blindness), Moscow, 1956.
2. Kravkov, S.V. Tsvetovoye zreniye (Color Vision), USSR Acad. Sci. Press, Moscow, 1951.

3. Rabkin, Ye. B. Tsvetorazlicheniye pri monokulyarnom i binokulyarnom zrenii (Color Discrimination in Monocular and Binocular Vision.) Proceedings of the 2nd All-Union Conference of Ophthalmologists. Tbilisi, 1961, p, 392.
4. Dalton, J. Mem. Lit. Phil. Soc. Manchester, 5/1, 18, 1798.
5. François, J. L'hérédité en ophthalmologie (Heredity in Ophthalmology) Paris, Masson, 1958.
6. Huddart, J. Phil. Trans. 67, 260, 1777.
7. Khernian, R. Proc. Internat. Congr. Human Genetics. Copenhagen, 1956, p. 722.
8. Lort, M. Phil. Trans. (London) 68, 612, 1778.
9. Pickford, R.W. Brit. J. Physiol. Optics 14, 2, 1951.
10. Pickford, R.W. Proc. Ann. Meet. Brit. Assn. Adv. Science, 1958, p. 104.
11. Polani, P.E., M.H. Lessop and P.M.F. Bishop. Lancet 50, 118, 1956.
12. Segal, J. Mechanismus des Farbenscheus (Mechanism of Color Blindness). Gustav Fischer Verlag, Jena, 1957.

Research Institute of Defectology
Academy of Pedagogic Sciences of the RSFSR



MICROINTERVAL ANALYSIS OF THE DEVELOPMENT OF VISUAL PERCEPTION

P.O. Makarov

Results of a microinterval analysis showing a regular phased development of human visual color perception. The stages involved consist of preperception, achromatic perception, and chromatic perception. This pattern is evident in color discrimination in the presence of two stimuli. When two short stimuli (initially red and then green) sequentially affect the same retinal region, then the intensification of one (green) masks the appearance of the other (weaker red) stimulus.

DEVELOPMENT OF COLOR PERCEPTION

/ 57

Every adequate optical and electrical stimulus gives rise to functional changes in the human visual system. Functional changes in the nerve cell and nerve fiber in response to a single stimulus are characterized by changes in a number of biophysical parameters: permeability, ion currents, electrical conductance, heat production, and electrical properties, and also by changes in threshold which have been described as a sequence of absolute and relative refractoriness and of supernormal (what N.A. Vvedenskiy describes as exaltation) and subnormal excitability. These fundamental characteristics of neuronal activity in sensory systems are also manifested in phases of perception.

As I have pointed out, the response of the visual system to two electro-optical stimuli consists of: 1) a phase of initial summation, 2) a phase of absence of summation resembling the refractory phase of a nerve, 3) a phase of secondary summation, and 4) a phase of discreteness, when, on the basis of his sensations, the subject concludes that the stimuli are double. It can be arbitrarily taken that the first stimulus produces the changes and second tests them. The critical interval of duplication reflects the rate of appearance of its sensation in the sensory sphere and serves as an index of the functional state of the system.

The results of experiments in which an optical adequatometer was used to present two flashes (wavelength 5160 Å, duration 4 msec, intensity of each 20 rheobases) to a dark-adapted human eye are shown in Fig. 1. If the interval between

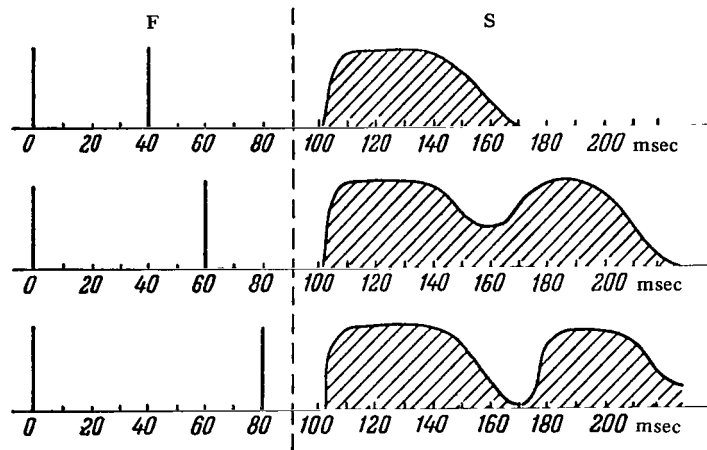


Figure 1. Effect of Interval Between Two Colored Flashes on Character of Visual Sensation.

Abscissa, Time in msec. F denotes Stimulation with Colored Flashes, S denotes Response Sensations. Oblique Shading corresponds to Sensation of Green Color.

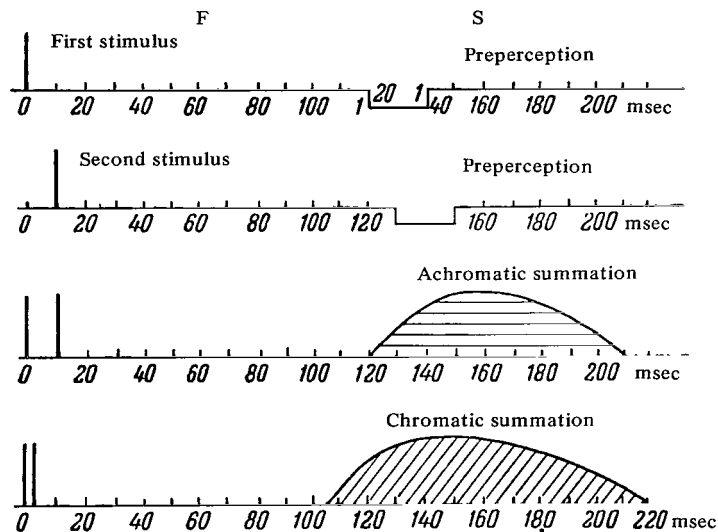


Figure 2. Effect of Summation of Subthreshold Stimuli on Color Perception. Legend as in Fig. 1.

flashes is 40 msec, the subject is aware of only a single sensation of a green color. If the interval is 60 msec (the middle part of Fig. 1), the subject declares that the flash which he perceives is beginning to split into two. This

means that the critical interval of discreteness (CID) is 60 msec. Functional mobility (FM) is expressed by the formula:

$$FM = \frac{1000 \text{ msec}}{CID} = \frac{1000 \text{ msec}}{60 \text{ msec}} = 16.7.$$

If the interval between the same stimuli is increased to 80 msec (lower part of Fig. 1), the splitting of the stimulus into two becomes more marked. If the same color stimuli (Fig. 2) are applied at an intensity slightly below threshold, each of them separately will produce no sensation. However, if the interval between them is 10 msec, an achromatic sensation arises through summation. If the interval between the same subthreshold green flashes is shorter (2 msec), a sensation of a green flash arises as a result of summation.

/58

Consequently, a subthreshold colored stimulus, acting in the present case 8° from the fovea on an area measuring 3.2°, evokes a chain of processes on the border of sensation; a second, similar subthreshold colored stimulus, as the result of summation of its effect with the effect of the first stimulus, evokes a chromatic sensation if the intervals are short and an achromatic sensation if they are longer. Consequently, each single stimulus near threshold level evokes a series of processes which precede perception. These preperception processes can be summated in microintervals of time and can give rise to perception. The whole cycle of development of color perception thus passes through a series of phases: a phase of preperception, a phase of achromatic perception, and a phase of chromatic perception.

/59

DEVELOPMENT OF VISUAL PERCEPTION DURING MASKING

Let us now consider interaction between two brief colored stimuli, in the case of retrograde masking, when the second (stronger) stimulus suppresses the effect of the first (weaker) stimulus within a certain range of time intervals.

The phased evolution of chromatic perception in a person with normal vision is illustrated in Fig. 3. The dark-adapted eye is stimulated by two flashes: red ($\lambda = 610 \text{ m}\mu$), intensity 2 rheobases, duration 5 msec, and green ($\lambda = 510 \text{ m}\mu$), following the first flash after intervals increasing from 20 to 80 msec. Its intensity is 100 rheobases, and its duration also 5 msec. During the action of these colored stimuli on the retina of one eye in the region of the fovea, and with an interval of 20 msec between them, a sensation of yellow-orange color appears, this is the phase of mixing of colors known in physiology and biophysics of vision.

The same flashes, with an interval of 35 msec between them, evoke a sensation of green, corresponding only to the second (stronger) masking stimulus. With this interval the effect of the first stimulus is masked, or suppressed, by the second. Masking is also observed with an interval of 55 msec between flashes. This is the phase of dominance of the strong stimulus over the weak. However, if the interval between stimuli is 75 msec (Fig. 3, lower part), the third phase appears. This is the phase of precise differentiation of chromatic color preception: the person sees first the red, then the green flash.

/60

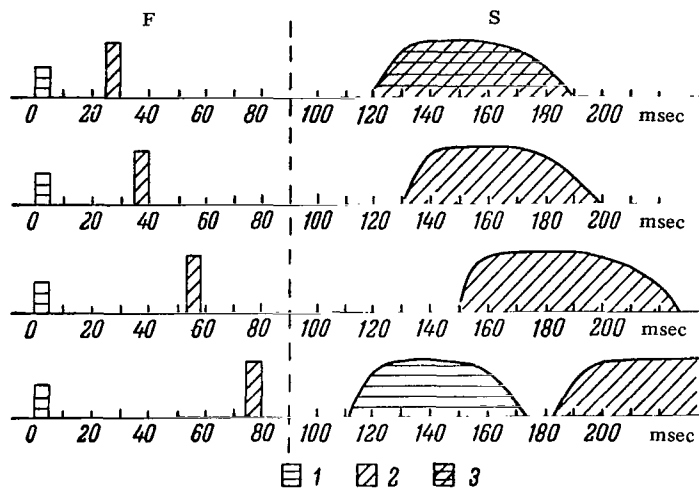


Figure 3. Phased Evolution of Chromatic Perception in Man with Normal Vision.

1 - Red; 2 - Green; 3 - Orange Color. Remainder of Legend as in Fig. 1.

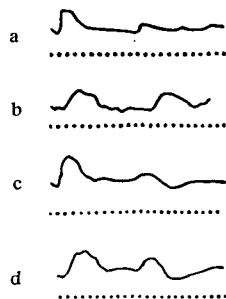


Figure 4. Electretinogram During Action of Two Colored Stimuli on the Human Eye.

Bottom Curve: Time Calibration, 4 msec. Explanation in Text.

Two colored stimuli of different chromaticities and intensities, acting on the central part of the retina, thus evoke a definite and reproducible sequence of phases depending on the duration of the microinterval between them: the first phase of color mixing, the second phase of dominance (suppression) of the weak stimulus by the strong as in masking, and the third phase of precise differentiation between the two stimuli as regards both their color and their order.

Depending on the microinterval of time between the stimuli, the phased character of evolution of visual perception can be clearly seen (Figs. 1, 2, 3).

The electretinogram (ERG) obtained during exposure to colored stimuli is shown in Fig. 4. In curves b and d the first and second stimuli are equal, but in curves a and c the first stimulus is stronger than the second. The interval between them is 65 msec. The latent period of the second response (the b wave of the electretinogram) on curves a and c in Fig. 4 is longer than on curves b and d.

The ERG, of course, cannot reveal the whole dynamics of the onset and formation of color perception, but the discontinuity of the retinal potentials corresponds to the discontinuity of the colored stimuli presented.

SUMMARY

1. Microinterval analysis of the development of colored visual perception in man by means of the technique of adequatometry reveal the existence of a series of successive phases: 1) preperception, 2) achromatic perception, and 3) chromatic perception.
2. Functional mobility of the human visual system and its changes in various diseases, fatigue, work, and sport can be judged from the critical interval of discreteness.
3. Investigation of masking in relation to the microinterval between colored stimuli revealed the following phases: 1) Mixing of the colors of the two stimuli, 2) dominance of the weaker colored stimulus by the stronger, 3) differentiation of the stimuli by color and order.

Department of Biophysics,
Leningrad State University

INVESTIGATION OF THE CRITICAL DISCRETENESS INTERVAL OF THE VISUAL SYSTEM

L. P. Grigor'yeva and Ye. N. Sokolov

Investigation of the critical discreteness interval, i.e., the minimum time interval in which it is still possible to discriminate successive visual stimuli. Studies involved the dependence of the interval on the location of the stimulus in the field of view, flare brightness, and conditions of adaptation. Significant shortening of the interval is demonstrated with increasing density of the receptor nerve elements of the retina, with increasing intensity of the afferent signal, and with rhythmic stimulation of the visual system.

Visual perception of surrounding objects is formed on the basis of two types of discrimination; spatial and temporal. The temporal aspect of visual discrimination is a problem to which increasing attention is being paid at the present time. This is because of technical developments and the appearance of new types of work during which a subject must perceive a large number of visual stimuli within a limited period of time. The object of the present investigation was to isolate and study the temporal aspect of visual discrimination. /61

To investigate temporal discrimination, Makarov [4, 5] has suggested and developed a method of discretometry. The writers have investigated the critical discreteness interval (CID) for individual areas of the field of vision. Local measurement has many advantages over measurement of the CID for the whole field of vision. If this method is used, the investigation can be conducted against the background of a more stable functional state of the visual system, temporal characteristics of different parts of the field of vision can be studied, and, as Makarov [5] has pointed out, the factor of labilization of the visual system can be excluded.

The dependence of CID on the location of the stimulus in the field of vision, brightness of the flashes, and conditions of adaptation was studied. In addition, the effect of repetitive photic stimulation on the minimum time interval during which discrimination is possible was investigated under normal conditions and in subjects with diseases of the eye.



Since the CID characterizes the cycle of recovery of excitability of the visual system to the original functional level after the action of the stimulus [8], an attempt was made to determine the functional significance of this criterion under normal conditions and in various diseases of the eye.

METHOD

Local stimulation of different parts of the field of vision was carried out by means of a capillary flash bulb mounted in a projection perimeter (PRP). The flash bulb was connected to the electronic circuit of a photostimulator, giving flashes with a duration of $13 \mu\text{sec}$. The photic characteristics of flashes from the bulb projected on to the surface of the perimeter arc were determined by oscillographic recording of the photoelectric currents by means of the UIF-1 VNISI instrument. The product of the luminance and the duration of the flashes visible at an angle of 0.2° , 0.5° , and 0.9° on the perimeter arc was 5.53×10^{-2} nit.sec. and 10.2×10^{-2} nit.sec. CID was measured in a lightproof chamber after adaptation for 3 min to a brightness of 400 nit and after adaptation for 10 min to the background brightness of the surface of the perimeter arc, namely 0.45 nit. During the experiment the investigated eye was located precisely in the center of the perimeter arc. Accuracy of observation of the object of fixation was verified by an optical method provided in the PRP. The subject was presented with paired flashes at time intervals of 10, 20, 30, 40, ... 200 msec between the two flashes. The CID was measured four times in each test area of the field of vision by the method of minimal changes. After analysis of the results the probability of visual discrimination of two consecutive flashes was calculated. Curves of probability of visual discrimination, calculated on the basis of 40 or more measurements for each interval between flashes, were plotted for the separate groups of subjects.

/62

In an investigation using Makarov's method [4], the coefficient of labilization (CL) of the visual system was calculated as the ratio between the minimum time interval capable of discrimination, measured by the method of paired flashes (the CID) and the duration of the interval obtained by measuring the critical flash fusion frequency (CFF). Altogether 10 subjects with a visual acuity of 1.0 and emmetropic refraction and also 64 subjects aged 12—17 years with diseases of the eye, were investigated.

RESULTS

a) Characteristics of Local CID Under Normal Conditions. Investigation of the dependence of CID on stimulus location in the field of vision in a temporal direction from center to periphery revealed a gradual (from 80 msec in the center to 190 msec at the far periphery) increase in time intervals within which discrimination of two flashes becomes reliable (Fig. 1). The steepness of increase of probability of visual discrimination is reduced at the periphery, and the range of scatter of values of time intervals determining discrimination, from the practically possible ($P > 0.01$) to the reliable ($P = 1.0$) is increased, evidence that discrimination of consecutive flashes is impaired.

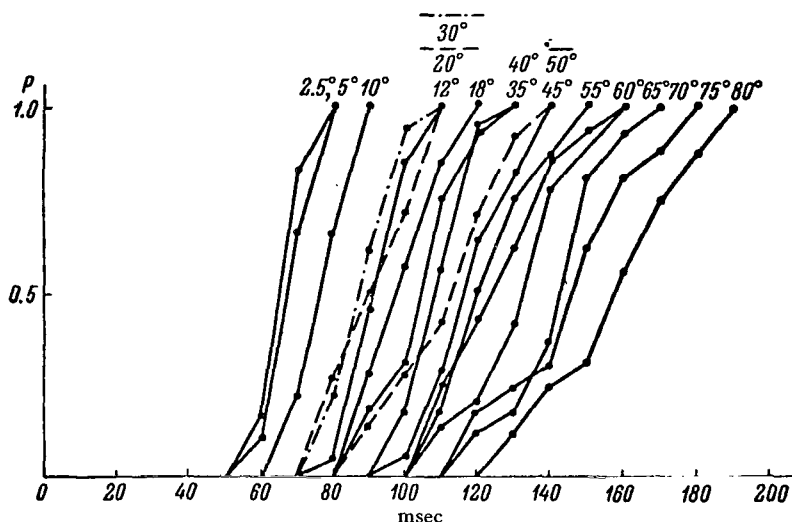


Figure 1. Curves of Probability of Visual Discrimination of Paired Flashes for Temporal Direction of Horizontal Meridian of Visual Field.

Abscissa, Intervals between Flashes, msec; Ordinate, Probability of Discrimination of Two Flashes. Areas of Visual Field in Which Measurements were made are Indicated Above.

Changes in the probability of visual discrimination followed the same pattern for the nasal, superior, and inferior meridians of the visual field. The threshold value of CID for $P = 0.5$ increases from the center to the periphery of the visual field in all meridians tested (Fig. 2). The threshold level of temporal level of discrimination is lower for the nasal than for the temporal direction and lower for the upward than for the downward direction. The better development and higher density of receptor nerve elements in the upper nasal regions of the retina compared with the lower temporal [14, 12] corresponds to the higher level of temporal discrimination in these areas. The character of the change in CID values in the direction from the center to the periphery of the retina correlates more closely with the density of distribution of ganglion cells in the human retina [12] (Fig. 3a) than with the distribution of cones [14] (Fig. 3b).

/63

With an increase in the brightness of the stimulus, the CID is shortened ($P = 1.0$) for the central, paracentral, and peripheral areas of the visual field (Fig. 4). The decrease in CID is proportional to the logarithm of intensity of the photic stimulus.

After adaptation for 3 min to light with a luminance of 400 nit, the values of CID reach their minimum (Fig. 4). In the course of dark adaptation for 30 min, a marked increase in CID was observed for parts of the central (2.5°), paracentral (15°), and peripheral (60°) zones of the visual field (Fig. 4). The increase in duration of CID was particularly marked in the first 10–15 min of dark

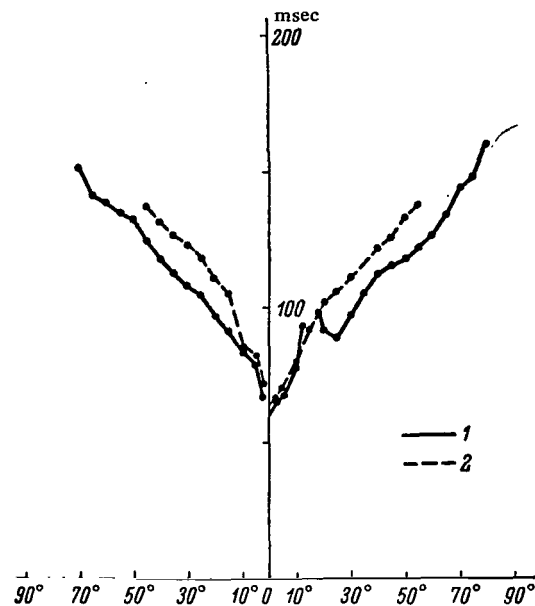


Figure 2. Dependence of Threshold Values of CID (msec) for $P = 0.5$ on Location of Stimulation in Visual Field for Temporal, Nasal, Upper, and Lower Directions.

Left: Vertical Meridian, Right: Horizontal Meridian. 1 - Temporally and Downward, 2 - Nasally and Upward.

adaptation. Local interrupted stimulation (20 Hz) of the tested areas of the visual field with light of the same intensity for 1 min led to a sharp decrease in the duration of CID. Values of CID measured immediately after such stimulation were close to the values of CID measured after light adaptation of the whole visual field. It must be emphasized that this principle applied during investigation not only of central and paracentral vision, but also of peripheral vision (Fig. 5). Control measurement of CID 5 min after repetitive stimulation showed that the level of CID activity attained after 30 min of dark adaptation is restored.

b) Characteristics of Local CID for Central Vision of Children with Defective Eyesight. The level of temporal discrimination depends on the character of the underlying disease of the eye. In children with myopia (16 cases), but with no pathological changes in the optic fundus, the field of vision, or accompanying diseases the CID values were normal (Fig. 6b). In 29 cases of complicated myopia combined with strabismus, amblyopia, or pathological changes of the optic fundus and visual field, the CID was considerably higher than normal (Fig. 6c). The highest value of CID (Fig. 6d, e) was obtained in 13 cases of optic atrophy and 6 cases of degeneration of the macular region.

/65

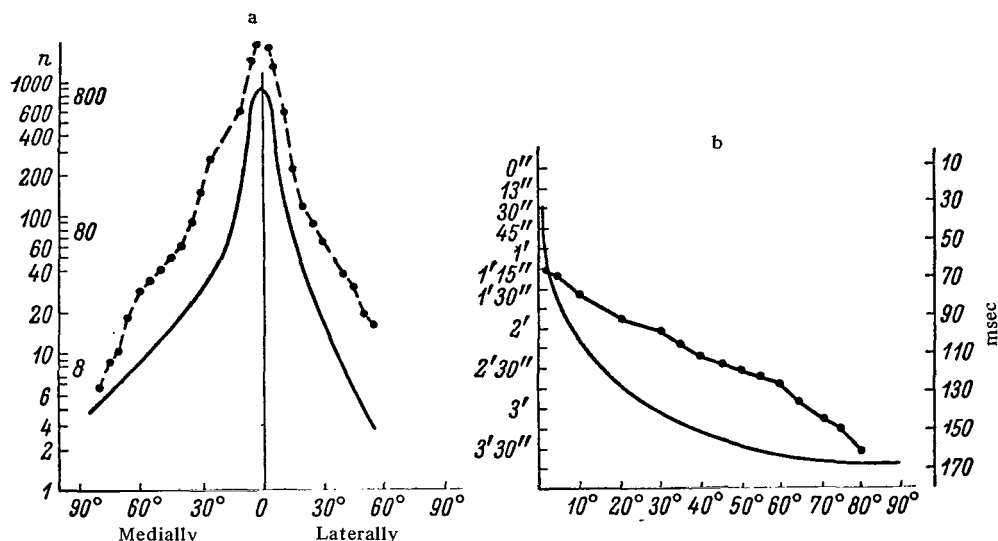


Figure 3. Distribution of Ganglionic Cells and Cones in the Retina.
a - Continuous Line Shows Density of Distribution of Ganglionic Cells along Horizontal Meridian of Retina, after Buren [12]; Broken Line Shows Changes in Threshold Values of CID ($P = 0.5$) along that Meridian; b - Curve Showing Changes in Distance Between Cones in Retina (Bottom Line), from Data of Polyak [14], and Changes in Threshold Values of CID (Top Line). Abscissa: Angular Distance from Center of Retina; Ordinate, on Left: Mean Angular Distance between Cones, on Right: CID, in msec.

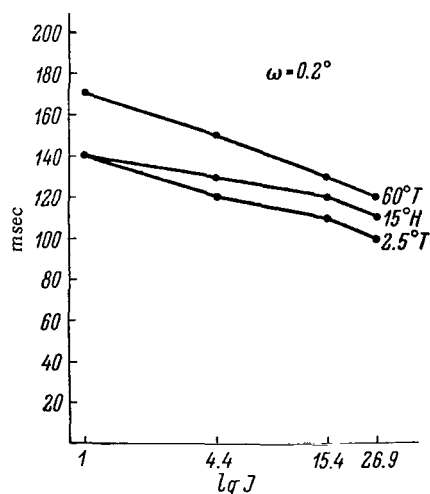


Figure 4. Dependence of CID ($P = 1.0$) on Brightness of Test Object for Areas of Central, Paracentral, and Peripheral Regions of Visual Field.

Abscissa: Brightness in Relative Logarithmic Units, Ordinate: CID in msec. Parameter of Curves is Angular Distance from Center of Retina; T indicates Temporal Direction; N Nasal Direction.

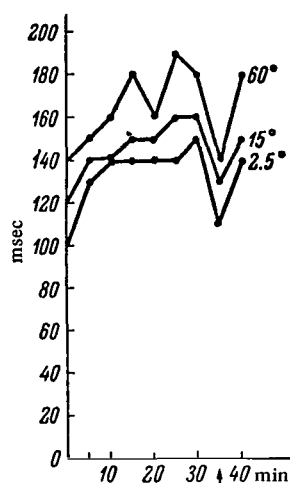


Figure 5. Curves of Change in CID ($P=1.0$) during Dark Adaptation for 30 Min, after Local Interrupted Stimulation ($f=20$ Hz), and after Dark Adaptation for 5 Min after Stimulation.

Arrow under Graph Indicates Local Interrupted Stimulation. Measurements made at 2.5, 15 and 60° in the Temporal Direction of the Visual Field.

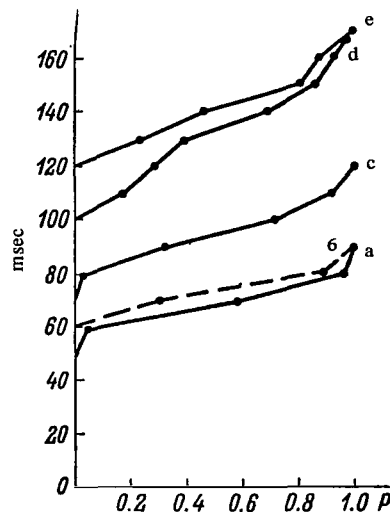


Figure 6. Curves of Probability of Visual Discrimination between Two Flashes by Subjects with Diseases of the Eye for Central Vision.

a - In Emmetropia; b - In Cases of Anomalies of Refraction without Pathological Changes in the Optic Fundus; c - In Myopia with Pathological Changes in the Fundus; d - In Cases of Optic Atrophy; e - In Degeneration of the Macular Region of the Retina. Parameters of Stimulus: Luminance 10.2×10^{-2} nit.sec; Size of Spot on Retina 0.9° ; Distance from Center 2.5° in Temporal Direction.

Values of the CID thus correspond to normal indices in cases of defective eyesight due entirely to anomalies of refraction of the eye, and the duration of the CID is increased in those eye diseases where morphological changes affect the iris and optic nerve. Since a disturbance of the optical system of the eye has no effect on the value of the CID, it is possible to verify the integrity of the nervous apparatus when a disturbance of the organ of vision is present.

The results of investigation of labilization in children with normal vision showed that the coefficient of labilization at the periphery of the visual field is much smaller than in the center. Whereas in the center of the visual field (2.5° temporally) the arithmetic mean value of CL was 1.96, at the periphery of the visual field (60° temporally) the mean value of CL was 1.28. Disturbance of this

index depended on the type of lesion of the eye. The types of relationship discovered between CID, CFF, and CL are given in Table 1.

TABLE 1. Mean Values of Coefficient of Labilization (CL), Critical Interval of Discreteness (CID), and Interval during Measurement of Critical Fusion Frequency (CFF) for Groups of Subjects with Two Positions of Test Spot in Field of Vision: 2.5° Temporally and 15° Nasally.

Diagnosis	Number of Subjects	2.5° Temporally			15° Nasally		
		CID	CFF	CL	CID	CFF	CL
Emmetropia	7	80	40.8	1.96	98.5	50	1.98
Myopia, hypermetropia	15	85.3	43.4	1.97	104	51.2	2.03
High Myopia	10	109	51	2.15	112.2	57.7	1.95
High Myopia, Optic Atrophy, Degeneration of Macula	19	126.3	119.2	1.08	118.7	134.1	0.956

In one group of cases with myopia and hypermetropia, the values of CID, CFF, and CL corresponded to normal. In cases of high myopia, optic atrophy, and degeneration of the macular region, a considerable increase in the duration of the intervals of temporal discrimination was combined either with a sharp decrease in CL or with its total absence. A special place is occupied by the effect of an increase in CID 15° nasally under conditions of repetitive stimulation, corresponding to a value of CL less than unity.

Children with high myopia in whom the CID was considerably increased, but the CL was normal, formed a separate group. The interval of temporal discrimination measured in these children during repetitive stimulation was much shorter than the interval of discrimination of paired flashes, and corresponded to the normal.

/66

DISCUSSION

Many parallels have recently been established between psychophysiological data and processes taking place at the neuronal level [10]. Participation of lateral inhibition strengthens successive and simultaneous contrast in the eye of the horseshoe crab [7, 8]. The presence of lateral inhibition has also been demonstrated in the vertebrate retina [11, 13]. These phenomena are not confined to the retina: the cycle of recovery of excitability in neurons of the visual cortex after exposure to flashes is phased in character [2, 6]. Jung [10] showed that during the action of flashes and in the dark interval between flashes, reciprocal B and D systems of neurons in the cat visual cortex respond by activation or inhibition, increasing the contrast of illuminance in time.

On the basis of his experimental data showing similarity between the activity of motoneurons and ganglion cells of the retina, Byzov classes the latter as neurons of the classical type. It can accordingly be postulated that the decrease in number of synaptic contacts at the level of the ganglionic layer of

the retina associated with a decrease in cell density in the direction toward the periphery [12] and the decrease in density of the horizontal cells [15], determine the low level and the high degree of scatter of the time for development of inhibition. The increase in duration of the cycle of recovery of excitation in the direction from center to periphery of the field of vision is evidently due to a decrease in lateral or reciprocal inhibition. This same mechanism also lies at the basis of lengthening of the recovery cycle after dark adaptation. During dark adaptation, lateral inhibition in the retina of the frog and cat becomes weakened and disappears completely [11]. The cause of this phenomenon is a decrease in inhibitory interconnections in the retina in darkness. The considerable increase in duration of the critical interval of discreteness in cases of retinal pathology (degeneration of the macula, high myopia with pathological changes in the optic fundus), also point to a role of the retina in the formation of the recovery of excitability cycle in the visual system.

A decrease in density of nerve cells is equivalent to weakening of the stimulus. This coincides with an increase in CID from the center to the periphery of the visual field. Under the influence of tetanic stimulation, mobilization of the synapses takes place and this is equivalent to strengthening of the stimulus. This potentiation effect is evidently due to a sharp decrease in duration of the excitability recovery cycle after local stimulation of the visual system by flashes.

The decrease in the range of labilization at the periphery of the visual field in children with normal eyesight is also connected with weakening of the mechanism of post-tetanic potentiation in that area, because the smaller number of synapses will lead to a lower degree of potentiation than in the case of a large number of synapses under the same conditions of tetanic stimulation. Prolongation of the excitability recovery cycle and the almost complete absence of labilization in high myopia, optic atrophy, and degeneration of the macula are evidence of a disturbance of synaptic transmission in these cases during the action not only of repetitive, but also of single stimuli. This is evidently caused by inadequate or delayed mobilization of the mediator from the presynaptic ending, as occurs with degenerating nerve fibers [3].

On the basis of microelectrode neurophysiological investigations a hypothesis can be put forward to explain potentiation of postsynaptic inhibition [9]. The psychophysiological data given in this paper when compared with the published results of investigations of neuronal processes demonstrate that the mechanisms of lateral and reciprocal inhibition and of their post-tetanic potentiation play a role in the system of temporal contrast. /67

On the basis of the facts described above it can be postulated that there are common neuronal mechanisms responsible for visual acuity, or the resolving power of the eye in space, and for the magnitude of the CDI — the index of resolving power of the eye in space, and for the magnitude of the CDI — the index of resolving power of the eye in time. Visual acuity diminishes from the center of the visual field to the periphery and with a decrease in brightness of the perceived object. As the results described in this paper have shown, temporal discrimination of paired flashes likewise deteriorates with a decrease in their brightness and with displacement of the measurements from the center to the periphery of the visual field. Visual acuity rises with an increase in brightness. Temporal

discrimination also improves considerably after adaptation to a high level of illumination. Under all these conditions, strengthening of inhibition is evidently a common basis for improvement of visual acuity and temporal discrimination.

CONCLUSIONS

1. Investigation of the CDI, an index of the cycle of recovery of excitation of the visual system under different conditions of local stimulation in persons with normal vision, revealed a marked decrease in duration of the CDI in the center of the retina with an increase in the intensity of the afferent signal, and also in cases of repetitive stimulation of the visual system.
2. Analysis of the results of measurement of the recovery cycle in diseases of the eye revealed an increase in the duration of the cycle of recovery of excitation in cases of pathological changes in the retina and optic nerve. Disturbances of the optical system of the eye had no effect on the CDI.
3. It is postulated that mechanisms of inhibition and post-tetanic potentiation participate in the formation of the cycle of recovery of excitability of the visual system and that the duration of this cycle in the visual system is an index of "temporal visual acuity."

REFERENCES

1. Byzov, A.L. *Elektrofiziologicheskiye issledovaniya setchatki* (Electrophysiological Investigations of the Retina), Moscow, 1966.
2. Kondrat'yeva, I.N. *Zh. Vyssh. Nervn. Deyat.* (Journal of Higher Nervous Activity), 15, 1, 1965.
3. Kostyuk, P.G. and L.A. Savos'tkina. *Fiziol. Zh. SSSR* (Physiological Journal of the USSR), 52, (7), 795, 1966.
4. Makarov, P.O. *Neyrodinamika cheloveka* (Human Neurodynamics). Meditsina Press, Leningrad, 1956.
5. Makarov, P.O. *Tezisy 1-oy nauchnoy konferentsii po prakticheskomu ispol'zovaniyu elektrofiziologicheskikh issledovaniy organa zreniya v oftalmologii* (Abstracts of Proceedings of the 1st Scientific Conference on the Practical Application of Electrophysiological Investigations of the Organ of Vision in Ophthalmology), Moscow, 1964, p. 38.
6. Polyanskiy, V.B. *Tezisy 5-go soveshchaniya po fiziologicheskoy optike* (Abstracts of Proceedings of the 5th Conference on Physiological Optics), Moscow, 1966, p. 116.
7. Ratliff, R. In: *Teoriya svyazi v sensorykh sistemakh* (Theory of Communication in Sensory Systems), Moscow, 1964, p. 338.
8. Hartline, H. In: *Current Problems in Biophysics*. 2, 263, 1961.
9. Shapovalov, A.I. In: *Fiziologiya neyrona i sinapticheskoy peredachi* (Physiology of the Neuron and Synaptic Transmission), Kiev, 1966, p. 38.
10. Jung, R. In: *Teoriya svyazi v sensorykh sistemakh* (Theory of Communication in Sensory Systems), Moscow, 1964, p. 375.
11. Barlow, H., R. Fitzhugh and S. Kuffler. *J. Physiol. (London)* 137, 338, 1957.

12. Buren, I. Retinal Ganglion Cell Layer., Springfield, 1963.
13. Kuffler, S. J. Neurophysiol., 16, 37, 1933.
14. Osterberg, D. Topography of the Layer of Rods and Cones in the Human Retina, 1935.
15. Polyak, S. The Retina. Chicago, 1941.

THE RETINA AS AN INDICATOR OF CORTICAL INDUCTION PHASES

P. G. Snyakin and A. P. Anisimova

Results of a study of positive and negative cortical induction as estimated by the retinal mobility index. It is shown that retinal mobility is a good indication of induction intensity and can be used to express the activity of the acoustic, olfactory, and cutaneous analysors. Retinal reactions reflect the formation of human conditioned reflexes as well as the phases of positive and negative induction between the sensory centers.

It was Hering [9] who first observed the interdependence between excitability of individual areas of the retina. These phenomena of interaction he described as induction. The retina thus became the first object in which was found the special neurodynamic phenomenon subsequently discovered and investigated by Sherrington [8] in the activity of the spinal cord, and brilliantly described in the cerebral cortex by Pavlov [5].

/68

Temporary conditioned connections are reflected in the adjustment of receptors, and for that reason investigations into the functional mobility of the retina, responsible for the precise relationship between organism and environment, are extremely important. Such adaptive responses are regulated by unconditioned and conditioned reflex mechanisms and they determine the precision of adjustment of the retina of specific conditions of illumination.

It has previously been shown by Kurilova, Anisimova, Galuzo, and others [1—4], working in the writers' laboratory, that this process can be used as an index of human conditioned—reflex activity. The mobility of the retina, based on the threshold of area of stimulation, is a convenient quantitative test of the strength of a conditioned reflex.

The object of the investigation described below was to examine processes of cortical induction (positive and negative) both within the same analyzer and in its interaction with others, on the basis of conditioned responses of the retina. It was found that the mobility of the retina is a convenient index of the strength of induction. For instance, in the presence of constant, weak illumination or in total darkness for 30–40 min, the level of mobility of the retina is stabilized. This level is taken as the initial background in the investigation described below.



An increase in the intensity of illumination against a background of low brightness or the appearance of light against a background of darkness leads to changes in the level of mobility of the photosensitive elements of the retina. As Snyakin [6, 7] has shown, the threshold of area of stimulation, i.e., the minimum area of photic stimulation perceivable by the eye, is a convenient quantitative index of retinal mobility. Under these circumstances fixation on the red fixation point is essential. An increase in this threshold characterizes a tendency toward demobilization, which exists during an increase in the intensity of illumination, while lowering of the threshold, on the other hand, characterizes a tendency toward mobilization of the photosensitive elements of the retina, which exists during a decrease in the intensity of illumination.

Any conditioned stimulus (acoustic, olfactory, tactile, temperature, etc.), if combined repeatedly with subsequent reinforcement by an unconditioned stimulus (illumination for 5 sec), strengthens the conditioned reflex. This is shown by an increase in the threshold of area of stimulation of the retina. After 10-20 such combinations, a stable conditioned reflex is formed as the retinal response.

/69

The sound of a metronome (frequency 70/min, $M = 70^+$), the odor of vinegar, and mechanical stimulation of the skin at a frequency of 60/min, produced by pressure on a rubber bulb connected to a rubber cuff fixed on the left forearm ($D = 60$), were used as conditioned stimuli.

During the formation of positive and negative conditioned-reflexes of the retina, all cases of the appearance of induction of the widest possible variety were taken into consideration. Special tests for positive and negative induction were carried out in some cases after two or more experiments.

For instance, in an experiment on one subject (Table 1), the existence of successive negative induction, evoked by acoustic stimuli, was demonstrated (subject N. P.).

TABLE 1.

Conditioned stimulus	Strength of conditioned response	Reinforcement
M-70 ⁺	+0.90	Reinforced (light)
M-70 ⁻	+0.16	Not reinforced
M-70 ⁺	+0.42	Reinforced (light)
M-70 ⁻	0.0	Not reinforced
M-70 ⁺	+0.42	Reinforced (light)
M-70 ⁻	-0.40	Not reinforced

Table 1 shows the process of differentiation of sound intensity of a repetitive acoustic stimulus, a metronome beating at the rate of 70/min. A louder sound was reinforced successively by light, while the weaker sound was not reinforced. In the first case a conditioned increase in the threshold or area

of retinal stimulation by 0.90 is observed compared with the background threshold, while unstable differentiation increases the threshold of area of stimulation by 0.16. Differentiation then becomes complete, and the last test application of $M = 70^-$ gave a decrease in the threshold of area of stimulation by 0.40 below the initial background. In this experiment, consequently, the negative phase of induction is seen as a result of a stably reinforced positive conditioned reflex.

In another subject, in whom no differentiation was formed during many experiments, at the 41st application of the differential stimulus ($M = 70^-$), this stimulus was applied first in the experiment. After two tests a positive stimulus was given: the odor of vinegar (previously tested 37 times), and this was sufficient (Table 2) to achieve complete differentiation (subject N.K.).

TABLE 2.

Number of tests	Conditioned stimulus	Strength of conditioned reflex	Reinforcement
41	$M-70^-$	+0.44	Not reinforced
42	$M-70^-$	+0.43	Not reinforced
37	Odor of vinegar	+0.54	Reinforced (light)
43	$M-70^-$	0.0	Not reinforced
90	$M-70^+$	+0.71	Reinforced (light)

It is clear from the results in Table 2 that complete inhibition is present at the 43rd test as a result of a negative induction, which was produced by olfactory stimulation, for this stimulation was sufficiently associated with the positive stimulus.

/70

In other cases, when acoustic differentiation is stabilized to the utmost degree, inductive relationships are created between the cortical centers, with the consequent appearance of positive induction. For instance, stabilized acoustic differentiation was tested after a positive olfactory stimulus, the response to which was slight, but after the action of the inhibitory agent (Table 3), the strength of the response to the olfactory stimulus was increased almost four times (subject V.B.).

TABLE 3.

Conditioned stimulus	Strength of conditioned reflex	Reinforcement
Odor of vinegar	+0.15	Reinforced (light)
$M-70^-$	-0.10	Not reinforced
Odor of vinegar	+0.59	Reinforced (light)
D-60	+0.31	Reinforced (light)
D-24	+0.09	Not reinforced
D-60	+0.58	Reinforced (light)
$M-70^+$	+0.10	Reinforced (light)
M-50	0.0	Not reinforced
$M-70^+$	+0.18	Reinforced (light)

Successive positive induction can be seen from these results, in which the inhibitory agent evokes double the increase in strength of the conditioned-reflex response to cutaneous and acoustic stimuli.

Hence, under the influence of different factors, foci of increased inhibition or excitation can be created at analysor points of the cortex, forming an element in the complex cortical mosaic. This functional mosaic constantly reflects the phases of induction, representing one aspect of cortical activity.

If a motor or secretory method is used as a test of a conditioned reflex, the strength of negative induction cannot be expressed quantitatively, since the effect of inhibition is revealed only by the absence of a motor or secretory response. In our method the strength of negative induction can be expressed quantitatively. For instance, if the level of retinal mobility during dark adaptation in the course of an experiment is taken as relative zero, the strength of negative induction can be estimated from the decrease in this index below the zero level.

CONCLUSION

The retina can be an indicator of the analysor activity of the acoustic, olfactory, cutaneous, mechanical and other analysors. The degree of analysis can be precisely assessed on the basis of quantitative investigation of its mobility. Effector responses of the retina clearly reflect the formation of conditioned reflexes in man, the formation of differentiation between stimuli (acoustic, olfactory, tactile, etc.), and the development of extinctive inhibition and other indices of cortical activity.

Phases of positive and negative induction that can be estimated quantitatively are constantly found between analyzor systems in the cortical dynamics. Such inductive relationships between centers are observed during interaction between the organs of perception. These interactions play an essential role during orientation of animals and man in a diversely acting external environment.

Conditioned connections may exert their action on the level of sensitivity of the retina. Such connections, and their number is in fact infinite, are at times hidden from the observer and are taken as effects resulting from the action of incidental stimuli, resembling the external inhibition which Pavlov defined as a manifestation of induction.

/71

Often in research and in the course of medical examinations a decrease or increase in the sensitivity of the retina can be observed for no apparent cause. However, a careful investigation shows that such cases are principally based on conditioned-reflex mechanisms. For instance, the occupation, the work place, the actual processes of work, the time of day, and other factors acting indirectly, can leave their imprint on the level of visual function, on the state of preparedness of the visual system. Evidence of this is given by the writer's investigations of mobility of the retina in patients with wounds of various parts of the brain. These showed that frontal and perioccipital wounds do not cause such disturbances, although they lead to considerable diminution of the field of vision. In frontal and

perioccipital wounds, the patients usually complain of impairment of vision both with a high and with a low intensity of illumination. These complaints can be regarded as due to loss of the effector function of the retina. In all brain wounds, the patient's ability to analyze color is always affected.

All these findings demonstrate the wide extent of the cortical connections of the visual analyzer, and this must be taken into account when the causes of changes in visual functions are being determined and, in particular, when maximum precision in the working of the visual system is required.

REFERENCES

1. Anisimova, A.P. Byull. Eksperim. Biol. i Med. 37, 2, 3, 1954.
2. Galuzo, N.V. K voprosy o reflektornoy nastroyke setchatki glaza na razdrzheniye drugogo glaza (Reflex Adaptation of the Retina to Stimulation of the Other Eye), In: Voprosy fiziologii i patologii nervnoy sistemy. Trudy Instituta normal'noy i patologicheskoy fiziologii AMN SSSR (Problems in the Physiology and Pathology of the Nervous System. Transactions of the Institute of Normal and Pathological Physiology, USSR Academy of Medical Sciences) 8, No. 6, Moscow, 1962, pp. 70-72.
3. Kurilova, L.M. Byull. Eksperim. Biol. i Med. 35, 6, 1, 1953.
4. Kurilova, L.M. Kharakteristika adaptivnykh svoystv zritel'nogo analizatora po pokazatelyam poroga ploshchadi razdrzheniya v raznykh uchastkakh setchatki (Characteristics of Adaptive Properties of the Visual Analyzer Based on Indices of the Threshold of Area of Stimulation in Different Parts of the Retina), Candidate Dissertation, Institute of Normal and Pathological Physiology, USSR Academy of Medical Sciences, Moscow, 1953.
5. Pavlov, I.P. Lektsii o rabote bol'shikh polushariy golovnoy mozga (Lectures on the Work of the Cerebral Hemispheres) Lecture 8. Complete Collected Works, 2nd Edition, Vol. 4. USSR Academy of Sciences Press, Moscow-Leningrad, 1952, p. 144.
6. Snyakin, P.G. Funktsional'naya mobil'nost' setchatki (Functional Mobility of the Retina). Medgiz, Moscow, 1948.
7. Snyakin, P.G. Metod funktsional'noy mobil'nosti v eksperimente i v klinike (The Method of Functional Mobility in Experimental and Clinical Practice) Medgiz, Moscow, 1959.
8. Sherrington, C. Reflektonnaya deyatel'nost' spinnoy mozga (The Reflex Activity of the Spinal Cord), Moscow-Leningrad, 1936, pp. 81-131.
9. Hering, E. Grundzüge der Lehre vom Lichtsinn (Fundamentals of Light Perception), Berlin, 1920, p. 159.

Laboratory of Physiology and Pathology of the Sense Organs,
Institute of Normal and Pathological Physiology,
Academy of Medical Sciences of the USSR.



TIME OF VISUAL PERCEPTION UNDER THE ACTION OF THERAPEUTIC X-RAY DOSES ON THE DIENCEPHALO-HYPOPHYSIAL REGION

G. I. Nemtseyev and N. S. Kharon

Investigation of the visual perception time in 26 patients subjected to x-ray treatment of the diencephalic region. Seventeen patients suffered endocrine exophthalmos and nine optochiasmal arachnoiditis with disturbed visual function. After irradiation all subjects exhibited reduced visual perception time, which is interpreted as resulting from a reduced excitability threshold of the interneuronal synapses of the visual tract.

The effects of ionizing radiation on the eye have been frequently investigated. Most of these studies deal with morphological changes in different parts of the eye, especially the lens and cornea. More recent studies have been devoted to the functional state of the visual system after exposure to various doses of x-rays.

/72

Arutyunyan and Ambartsumyan [1] studied the lability of separate components of the rabbit visual system in radiation sickness. The experiments were carried out on rabbits with electrodes implanted into the cortex and subcortical visual nuclei. Electrophysiological investigations were undertaken with the use of repetitive photic stimulation. Besides the high reactivity and rapid restoration of functions in the cortex, changes in the subcortical nuclei began to be recorded 2—3 days later, and complete recovery of functions was not observed until 30 days later.

Tsy-pin [6] studied the state of components of the visual system in the course of acute radiation sickness due to whole-body and local irradiation of rabbits. He suggested that ionizing radiation in large doses has a paralytic action on the visual system, initially activating its electrical activity but subsequently inhibiting it.

Sikharulidze et al. [5] studied the temporal development of the successive image under normal conditions and in various eye diseases after irradiation of the skull in the projection zone of the occipital cortex with extremely small doses (1 R). In the group of healthy subjects the latent period of appearance of the successive image varied from 1 to 2 sec, and its duration from 10—20 sec.

After irradiation the latent period was reduced to zero and the duration of the successive image was 10 sec. In diseases of the optic nerve the duration both of the latent period and of the successive image was increased, but after x-ray irradiation both the latent period and duration of the successive image were reduced. Although in every case a regular pattern was observed (shortening of the latent period of the visual image), it is difficult to imagine that such micro-doses of radiant energy could have produced such changes, more especially because they were applied to the bones of the skull.

The effect of therapeutic doses of x-ray irradiation of the eyes on the electroretinogram (ERG) and certain visual functions has been studied only by Bogoslovskiy and Itsikson [2]. Their investigations of the visual functions and ERG undertaken in the course of long periods after the end of x-ray therapy showed that, despite very large total doses received by some patients (up to 11,000 R in three series over the period of 22 months, with a sessional dose of 200 R), no appreciable changes in the visual functions or ERG could be observed in the irradiated eye. On the basis of these findings they conclude that therapeutic doses of x-rays are harmless to the eye.

/73

Data in the literature show conflicting opinions with regard to the effect of x-ray irradiation (especially in therapeutic doses) on conductance in the visual nervous pathways.

One of the authors of this paper (G. I. N.), in the course of observations on changes in the visual perception time (VPT) in patients with diseases of the optic nerve, including two patients with diencephalitis, observed a shortening of VPT in both patients after therapeutic x-ray irradiation of the diencephalon [4]. This suggested that x-ray irradiation of the diencephalon affects conductance in the visual nervous pathways. The work of Nemenov [3] has shown that the diencephalo-hypophyseal region is highly sensitive to x-ray irradiation.

The object of the investigation described below was to study the effect of therapeutic doses of x-ray irradiation of the diencephalo-hypophyseal region on conductance in the visual nervous pathways.

METHOD

The VPT was measured by the method of error of localization with introduction of a correction for the stimulus summation time in the retina. In this way the total visual perception time could be obtained. The apparatus and method developed and described in detail by Nemtseyev [4] were used to measure the VPT.

As norms for analysis of the results, the limits of normal values of visual perception time for different age groups obtained in the same investigation on 108 healthy persons and subjected to statistical analysis were used (the limits were calculated with a confidence of 95%):



15 - 20 years: 50 - 80 msec
21 - 30 years: 51 - 81 msec
31 - 50 years: 57 - 85 msec
over 50 years: 65 - 89 msec

Since previous investigations [4] showed that the possible error of the method when measuring VPT is 4 msec, during analysis of the results only the difference between the results of measurements of VPT exceeding this figure were taken as an increase or decrease in the VPT.

X-ray therapy of the diencephalic region (for brevity in future this term will be used, although during x-ray therapy neighboring brain structures, especially the pituitary, are inevitably irradiated) was given from a type RUM-11 x-ray therapy apparatus: Voltage 182 kV, current 10 mA, filter 0.5 mm Cu + 1 mm Al, skin-focus distance 30 cm, tube 4×4 cm or 6×8 cm.

RESULTS

The visual perception time was investigated periodically in 26 patients; only the diencephalic region of 12 patients was irradiated, and the diencephalic region and both orbits in 14. The patients included 15 men and 11 women. Six patients were aged 15—20 years, three 21—30 years, nine 31—40 years, four 41—50 years, and four were over 50 years old (the division among age groups was the same as for previous measurements of VPT under normal conditions).

By the etiology of the disease the patients were divided into two groups.

/74

The first group — endocrine exophthalmos — contained 17 patients. In 17 of them clinical examination led to a diagnosis of bulbar encephalitis with the development of exophthalmos, and in two patients the exophthalmos was the result of a previous thyroidectomy. The most characteristic feature of the clinical picture of this group of patients was the presence of exophthalmos associated with a normal state of visual functions and of the optic fundus. In addition, this group included two other patients who received x-ray therapy for neoplasms (in one case a pituitary adenoma, and in the other an eosinophilic granuloma of the base of the temporal bone and orbit), so that the state of their visual functions was normal.

The second group (nine persons) included patients with optochiasmal arachnoiditis and lesions of the optic nerves resulting from it which, in their clinical picture, could be interpreted in two cases as retrobulbar neuritis and in the remaining seven cases as various transitional stages from neuritis to optic atrophy with characteristic changes in the optic fundus. All these patients showed disturbances of visual functions. In this group of patients x-ray irradiation of the diencephalo-hypophyseal region was thus carried out against the background of a pathological state of the optic nerves.

A total of 110 tests of visual perception time were carried out on the 26 patients*. The VPT was measured before the beginning of x-ray therapy, during therapy, and after its end.

During irradiation of the diencephalic region, and also of the diencephalic region and orbits, in the overwhelming majority of cases (23 of 26) a marked and regular shortening of the VPT was observed. In 13 of these 23 patients the VPT became less than the lower limit of normal toward the end of the course of x-ray therapy. In the only case when the VPT remained unchanged compared with its initial value at the end of the course of x-ray therapy (endocrine exophthalmos), a marked shortening of the VPT was observed after the first sessions of x-ray therapy, and it returned to the initial value after the second course of x-ray therapy (by the 25th session).

Of the two cases where the VPT was lengthened at the end of the course of x-ray therapy, one patient had optic neuritis and the second had optochiasmal arachnoiditis with incomplete atrophy of the optic nerves. In the second of these cases a clear shortening of the VPT was observed after the first ten sessions of x-ray therapy, and not until the 15th session was the VPT lengthened, when it became slightly (6 msec) longer than initially. Since the writer's previous investigations revealed lengthening of the VPT in patients with neuritis and incomplete optic atrophy, in neither of these cases could a combination of changes in conductance of the optic nerves on account of the dynamics of the pathological process together with the changes produced by x-rays be ruled out.

The effect of x-ray irradiation of the diencephalic region only and of combined irradiation of the diencephalic region and orbit on the value of the VPT was about the same. This suggests that the diencephalic region plays the most important role in the changes in VPT produced by therapeutic doses of x-ray irradiation.

With an increase in the dose of x-ray irradiation, the VPT of most patients was shortened. The effect of high antitumor doses could not be assessed because the mean total doses usually reached 1000 R and in five patients they were 1500 - 2100 R, and only in one patient with a pituitary tumor did the total dose reach 3000 R.

/75

Among the patients showing a shortening of the VPT, in six patients this took place at the beginning of treatment, after a stage of slight lengthening. During analysis of the dynamics of VPT in patients with pathological changes affecting the optic nerve and reduced visual acuity (the second group of nine patients) no definite relationship or parallel trend between the increase in visual acuity and shortening of the VPT could be detected.

The relative stability of shortening of the VPT after x-ray irradiation must be noted. In one patient the VPT could be measured one year after the end of

*Each test consisted of measurement of the VPT of both eyes.



irradiation, in one patient 7 months after, in one patient 5 months after, and in one patient 2 months after. In all four patients, the VPT was lower than it was initially, although a tendency was observed for its gradual return to its initial level.

DISCUSSION

During the action of therapeutic doses of x-rays on the diencephalo-hypophyseal region the visual perception time is shortened in the overwhelming majority of cases. Since this fact was established apparently for the first time, and conductance of the visual nervous pathway has not hitherto been investigated during x-ray irradiation (in particular, of the diencephalo-hypophyseal region), it is impossible to compare these results with those obtained by any other investigators. However, they do agree with information given in a brief survey of the literature concerning the activating effect of ionizing radiation on components of the visual system.

The diencephalic region may play a dominant role in regulating the excitability of the receptors, conducting fibers, and cortical centers of sensory systems, where its role is one of facilitation. It can also be considered that lowering of the threshold of excitability of interneuronal synapses of the visual system plays a leading role in the shortening of VPT observed after x-ray irradiation of the diencephalic region.

A much less important role can be ascribed to the direct action of x-rays on the conducting pathways (fibers of the optic nerve), for the shortening of the VPT persisted for quite a long time after the action of x-rays had ceased, and it was observed both in cases where the optic nerve was intact (diencephalic exophthalmos) and in cases where it was certainly involved in the pathological process (optochiasmal arachnoiditis).

CONCLUSIONS

1. After the action of therapeutic doses of x-rays on the diencephalic (diencephalo-hypophysial) region the visual perception time is shortened in the overwhelming majority of cases.
2. Shortening of the visual perception time is observed both when the optic nerve is intact and also when it is involved in the pathological process.
3. Shortening of the visual perception time is observed after the action of therapeutic doses of x-rays whether either the diencephalo-hypophyseal region alone is irradiated, or it is irradiated together with the orbits, and it must therefore be associated with changes in the diencephalic region.

REFERENCES

/76

1. Arutyunyan, R.K. and S.G. Ambartsumyan. Vopr. Radiobiol. (Problems of Radiobiology) 11, 43, 1961.
2. Bogoslovskiy, A.I. and L.Ya. Itsikson. Materialy II Vserossiyskoy konferentsii oftal'mologov (Proceedings of the Second All-Russian Conference of Ophthalmologists) Tbilisi, 1961, p. 247.
3. Nemenov, M.I. Vestn. Rentgenol. i Radiol. (News of Roentgenology and Radiology) 26, 1, 22, 1944.
4. Nemtseyev, G.I. Vopr. Neyrooftal'mol. (Problems of Neuroophthalmology) 10, 5, 1961.
5. Sikharulidze, I.A., R.I. Basilidze and V.K. Abuladze. Materialy II Vserossiyskoy konferentsii oftal'mologov (Proceedings of the Second All-Russian Conference of Ophthalmologists) Tbilisi, 1961, p. 248.
6. Tsypin, A.B. Med. Radiol. 5, 22, 1956.

Kharkov Research Institute of Work Hygiene and Occupational Diseases and
L.L. Girshman Kharkov Regional Eye Hospital



FUNCTIONAL EFFICIENCY OF THE VISUAL ANALYSOR DURING WORK WITH MICROSCOPES

N. I. Zoz

Working conditions and the functional efficiency of the visual analyzor were investigated in workers making semiconductor instruments in which several operations are performed with the aid of microscopes. Time and motion studies of the work process, investigations of the stability of color discrimination, visibility, and visual efficiency showed that the assembly of semiconductor instruments causes changes in the functions tested, and these changes increase throughout the working day. The quality of the lighting at such factories is reviewed and some recommendations given for its improvement.

In modern industry there are several operations associated with considerable strain on vision, such as the manufacture of small parts, the assembly of separate units and of precision instruments, and all operations requiring visual inspection. The efficiency of the visual analyzor during precision operations has been investigated many times both in the USSR and elsewhere. However, only a few of these investigations have been undertaken with the use of optical instruments.

/77

The investigation described below was a physiological study of the hygiene of working conditions during certain types of operations requiring visual strain. The workers concerned made many complaints of headache and unpleasant subjective sensations affecting the eyes. In this connection it was interesting to detect any changes in the functional state of the visual analyzor under industrial conditions during work using a microscope.

The investigation was carried out at a factory manufacturing semiconductor instruments. The reliability of these instruments is largely dependent not only on the technology of their manufacture, but also the quality of performance of work operations calling for considerable visual strain during discrimination of objects measuring less than 0.1 mm. Most operations were carried out on special equipment by means of the BMP-1 binocular microscope under a magnification of 8-32 times.

Modern manufacture of semiconductor instruments requires stable micro-climatic conditions, so that the workshops are housed in airtight buildings without natural light. The workshops have built-in illumination with luminescent lamps. The intensity of illumination at the work places reached 280-300 lx. For local illumination, incandescent lamps fixed in adjustable lamp holders which could be turned in the desired direction and microscope condensers were used. At some work places lamp holders with LDTs (2×15) luminescent lamps and transparent plastic diffusers were available. The luminance of the surrounding surfaces was 40-80 nit.

The work was complicated by the unpleasant sensation of reflected glare from the parts, especially in the field of vision of the microscope, and this was aggravated by the presence of bright spots on the glass covering the work tables, from the filaments of the incandescent lamps in clear glass bulbs. A questionnaire showed that only 18% of the answers to the questions were complaints of unsatisfactory lighting. The production process required discrimination between small components of the parts from which the instruments were made and the detection of faults. In the course of their work, the assemblers had to transfer their gaze from the microscope field to the instrument table and the oscilloscope screen — eight times per minute, and this was accompanied by readaptation and changes in accommodation.

/78

The investigations of the functional state of the visual analyzer were carried out at intervals during the working day under normal production conditions. Besides stopwatch observations, tests of visual efficiency were carried out by means of tables with Landolt's rings, visibility was measured by means of L. L. Dashkevich's polarization instrument (PBIV), and the functional stability of color vision was investigated with Ye. B. Rabkin's anomaloscope (ASR).

Two groups of women workers with normal vision and color vision, age 20-25 years, and with 3-5 years of experience at that particular job were investigated. The first group (12 persons) consisted of women performing work operations with a microscope, the second group (6 persons) women measuring the electrical parameters of the instruments. The tests were carried out during the working time in the first shift, four times in the course of the working day.

For 60-90% of their working time, the assemblers were engaged in work causing a strain on their vision. Detailed time and motion studies of their work showed no significant change in the time of assembling of each instrument in the course of the working day, indicating that the load was uniformly distributed during the shifts.

To investigate visual efficiency, tables containing 256 Landolt's rings, 2 mm in diameter, were used. The angular size of the gap in the ring was about 4'. The time required to carry the test and the number of mistakes were recorded. The first group of workers showed virtually no change in the time of performance of the tests during work, while those of the second group showed a significant increase. The number of errors made by both groups increased toward the end of the working day.

For comparison of the quantitative and qualitative aspects of visual performance the method of determination of the quantity of visual information, suggested by Kgek and Foytova [1], was used. The results are shown graphically in Fig. 1. Results of 50 observations were analyzed. As the graph shows, the results provide no evidence indicating a decrease in visual efficiency toward the end of the working day in the case of assemblers working with microscopes, whereas the second group of assemblers showed a very marked decrease. This method evidently was insufficiently precise for persons working with microscopes, because nearly all showed, at the same time, a decrease of visibility in their thresholds of contrast on the average by 20% compared with values obtained in the morning. The stability of individual functions of the visual analyser is regarded as a very important characteristic of functional state. We investigated the functional stability of color discrimination by means of a spectroanomaloscope for three equations in the middle and peripheral areas of the visible spectrum of radiation (equations: green-yellow, $\lambda 530 \text{ m}\mu : \lambda 580 \text{ m}\mu$, red-yellow, $\lambda 670 \text{ m}\mu : \lambda 580 \text{ m}\mu$; blue-yellow, $\lambda 475 \text{ m}\mu : \lambda 580 \text{ m}\mu$).

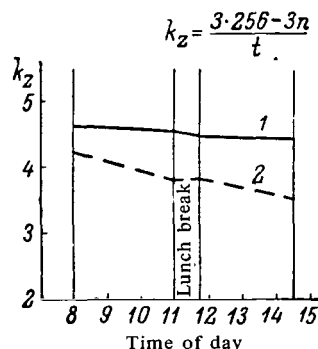


Figure 1. Changes in Visual Efficiency (k_z) in the Course of the Working Day.

1 - During Work with Microscope; 2 - During Measurement of Electrical Parameters of Instruments.

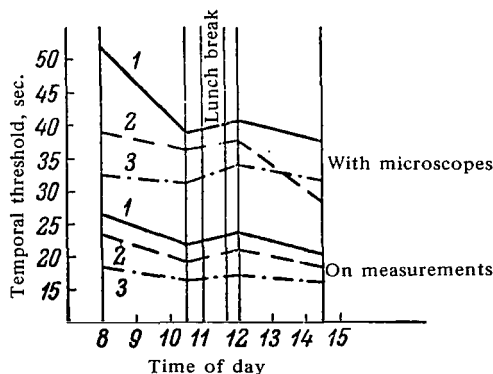


Figure 2. Changes in Stability of Color Discrimination in the Course of the Working Day, Determined from Spectral Equations.

1 - Green-yellow, $\lambda 530-580 \text{ m}\mu$;
2 - Red-yellow, $\lambda 670-580 \text{ m}\mu$;
3 - Blue-yellow, $\lambda 475-580 \text{ m}\mu$.

The level of functional stability of color discrimination is characterized by the phenomenon of adysparopia, which is determined by a temporal threshold. The mean values of the temporal threshold from 48 observations are shown graphically in Fig. 2. The decrease in the indices towards the end of the working day, compared with values obtained in the morning, can be regarded as significant with a level of probability of 99%. In relative indices, this decrease was 20-30%. The changes observed in this particular function did not recover completely during the lunch break, indicating their severity.

The need for readaptation, the work of the accommodation apparatus, and the presence of reflected glare in the field of vision, according to the findings of Kravkov [2], Samsonova [4], Meshkov [3], and other workers, considerably complicates visual work and leads to more rapid fatigue. As might be expected, therefore, physiological investigations conducted under actual production conditions demonstrated a significant falling off of visual functions. However, the statistically significant difference between the levels of functional stability of color discrimination among the investigated groups must be noted.

The results of the observations described above and of previous studies showing low level of functional stability of color discrimination in persons working under visual strain of different degrees suggest that permanent disturbance of the stability of color discrimination may arise during work involving prolonged visual strain.

CONCLUSIONS

1. The assembly of semiconductor instruments by means of microscopes requires great visual concentration throughout the working day.
2. The intensity of illumination of the work places is not in all cases in accordance with the standard laid down. The quality of illumination in some cases does not correspond to modern hygienic and lighting-engineering requirements.
3. Changes in the investigated functions of the visual analyzer do not recover fully during the lunch break and they increase in severity in proportion to the duration of visual work. To reduce fatigue in the course of the working day, additional statutory breaks in the work period were recommended.
4. The method used to assess the functional state of the visual analyzer, based on stability of color discrimination, revealed a statistically significant decrease in the level of this function in the course of work and confirmed that this method can be used as one of the criteria of assessment of work involving visual strain.

/80

REFERENCES

1. Kgek, I. and Ye. Foytova. *Svetotekhnika* (Light Engineering) 10, 23, 1964.
2. Kravkov, S. V. *Glaz i yego rabota* (The Eye and Its Work). Moscow—Leningrad, 1950.
3. Meshkov, V. V. *Osvetitel'nyye ustanovki* (Illuminating Systems). Moscow—Leningrad, 1947.
4. Samsonova, V. G. *Probl. Fiziol. Optiki* (Problems of Physiological Optics) 2, 54, 1944.

Institute of Work Hygiene and Occupational Diseases,
USSR Academy of Medical Sciences



II. ELECTROPHYSIOLOGY AND BIOPHYSICS OF VISION

SHORT-LATENCY PROCESSES IN THE VISUAL SYSTEM OF CATS

I. A. Shevelev

Early changes preceding the development of the initial afferent flow were studied at all levels of the visual system of anesthetized cats on the basis of integral slow potentials. Responses of very short latency were found in the ganglionic layer of the retina and at higher levels of the visual system, indicating the existence of a system of cells and fibers transmitting stimuli with very short delays (4-5 times quicker than the principal group). On the basis of similarity between the recovery cycle of cortical responses to electrical stimulation of the optic nerve and cortical prepotentials it is postulated that the latter are the result of changes in excitability of a small group of units with the shortest latency after their synchronized firing.

The work of Shevelev and Krol' [2] has shown that regular changes in excitability, most clearly marked in the cortex where they develop in cyclic fashion, arrive in the visual system of anesthetized cats a few milliseconds after a noiseless flash. This investigation conclusively confirmed the existence of an early afferent stimulus preceding the development of integral primary evoked potentials and modifying the state of the visual centers before they received the initial afferent flow. However, neither the mechanisms of this early afferentation nor the nature of the changes in excitability of the visual centers evoked by it can be clearly explained. Some additional data on this problem are described below.

/81

The first problem resulting from a previous discovery of a decrease in amplitude of the test response in the cortex 4-5 msec after a flash concerned the possibility of occurrence, and the nature, of such short-latency stimulation at the output of the retina. Experiments were carried out in which a macro-electrode was applied to the papilla of the optic nerve in the optic cup of an anesthetized cat after removal of the cornea, lens, and vitreous. Low-frequency (ERG) and high-frequency components of the response were filtered and recorded separately (Fig. 1: 2, 3). Determination of the integral of this multiple activity (Fig. 1: 1, 8) suggested that 8-10 msec after the beginning of the flash, inhibition

of background activity developed in the ganglionic layer of the retina. This phenomenon, called "pre-excitatory inhibition" by Granit [4], is connected genetically with P_{III} component of the integral ERG (response of horizontal cells or fast bipolars according to Byzov [1]).

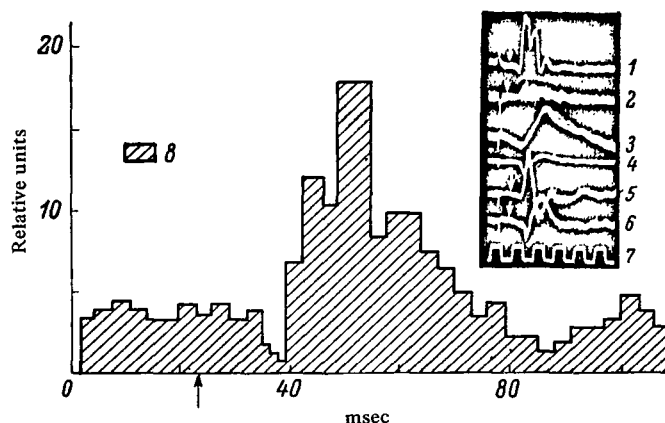


Figure 1. Early Responses in Different Parts of the Visual System.

Curves Obtained by Superposition of 20 Responses Recorded by Macroelectrodes; 2 - Global Neurogram; 3 - ERG from Papilla of Optic Nerve in Exposed Optic Cup; 4 - Responses in Optic Tract; 5 - Responses in Lateral Geniculate Bodies; 6 - Responses in Visual Cortex. Calibration; $100\mu V$, 50 Hz (7). Integral of Global Neurogram (2) Shown in Curve (1) and on Graph (8). On All Curves, Short Downward (2-6) or Upward (1) Deviation of Beam at Beginning of Scanning is Artifact of Flash. Arrows Indicate Beginning of Early Changes in Potential. On Graph, Abscissa: Time (in msec), Arrow: Time of Stimulation, Ordinate: Mean Power of Process Over 3.3 msec (in Relative Units). Results of Experiment on Cat Anesthetized With Sodium Amytal (NK-46).

It is interesting that sometimes early prepotentials can also be recorded by macroelectrodes at other levels of the visual system: in the lateral geniculate body (LGB) and visual cortex (Fig. 1:5, 6). The early inhibitory phase can also be clearly identified in responses of spontaneously active neurons in the visual centers (Fig. 2).

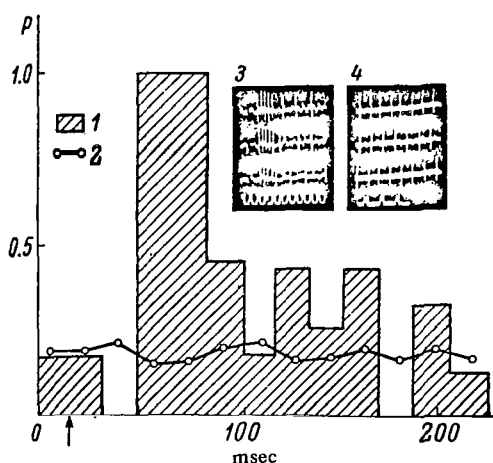


Figure 2. Histogram of Response of Unit 35KT (1) of Lateral Geniculate Body of Waking Cat Immobilized with Tubocurarine (BK-103 35KT), to Flash Lasting 100 msec with Intensity 42.7 dB above Threshold of Response for this Duration.

Abscissa: Time, in msec; Arrow Indicates Beginning of Flash; Ordinate: Probability of Appearance of Spike within 18.6 msec; 2) Distribution of Spontaneous Spikes in Background; 3) Tracings of Responses of this Same Unit (Gap in Isoelectric Line Denotes Switching on Light); 4) Its Background Spontaneous Activity. Time Marker 50 Hz (3) and 10 Hz (4).

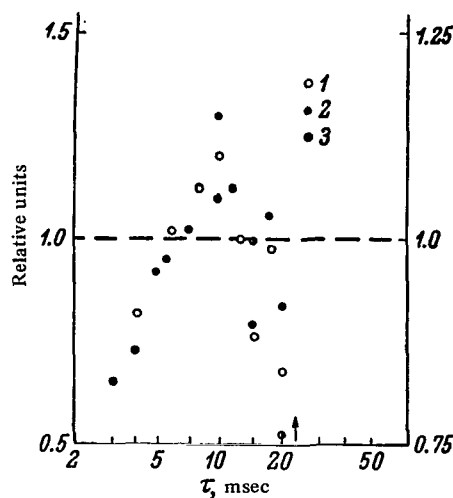


Figure 3. Temporal Course of Changes in Excitability of Visual Cortex after Photostimulation of Contralateral Eye of Anesthetized Cat during Testing by Electrical Stimulation of Optic Nerve (1), Optic Radiation (2), and during Electrical Stimulation of Optic Nerve with Paired Pulses (3).

Abscissa: Interval between Conditioning and Test Stimulus. Arrow Denotes Beginning of Development of Primary Evoked Potential to Light in Cortex (for 1 and 2). Ordinate: Changes in Magnitude of First Slow Postsynaptic Phase of Response to Test Stimulus. Ordinate on Left for Points 1 and 3, on Right for Points 2.

The second problem to be examined was precise determination of the temporal course of early fluctuations in excitability in the visual cortex where, according to the results of the previous investigation, they were most complex. The use of electrical stimulation of fibers of the optic radiation, and not of the optic nerve, and the test stimulus after the flash was considered to be stricter, because by the first method desynchronization of the test stimulus is reduced in its passage across synapses in the LGB, from nerve to LGB, and from LGB to cortex. The graph in which excitability of the visual cortex is plotted against time elapsing after the flash in front of the contralateral eye (Fig. 3:2) shows that the general course of changes in excitability before the beginning of development of the evoked potential through photic stimulation is the same as after testing by stimulation of the nerve (Fig. 3:1). The level of significance of these

/82

data is very high ($P < 0.01$). In connection with other experimental aims, the recovery cycle of responses of the visual cortex and other parts of the visual system was investigated during stimulation of the optic nerve by paired pulses [3]. The relationship between the relative magnitude of the first postsynaptic phase of the cortical responses to the second pulse and the interval between stimuli (Fig. 3:3) within the range from 1-20 msec was very similar to the course of pre-excitation (points 1 and 2 in Fig. 3). Differences concern primarily the degree of change in amplitude of the test response (within this temporal range it does not exceed $\pm 20\%$ during pre-excitation, and in the course of the cycle of excitability the changes may reach $\pm 50\%$).

It is considered that the facts described above can form the basis for a working hypothesis concerning the mechanisms of early changes in excitability in the visual centers. A signal from the retina (it may be negative, in the form of a decrease in background activity) reaches the LGB and cortex along the fastest-conducting fibers and causes a small group of units (judging from the small changes in excitability) to discharge. The short-latency units evidently receive a highly synchronized input signal and, as a result, the course of their integral recovery cycle, which we test by responses of electrical stimulation, is similar to that which takes place in the cortex after synchronous excitation of optic nerve fibers by electrical stimulation. This hypothesis, requiring careful verification at the cell level, attracts our attention to the mechanisms of possible transformation of an early negative signal into a positive one, and also to identification of the level of the system at which this phenomenon takes place, and determination of the temporal characteristics of early processes in these structures.

/83

REFERENCES

1. Byzov, A.L. *Elektrofiziologicheskiye issledovaniya setchatki* (Electrophysiological Investigations of the Retina). Nauka, Moscow, 1966.
2. Shevelev, I.A. and V.M. Krol'. *Zh. Vyssh. Nervn. Deyat.* (Journal of Higher Nervous Activity) **16**, 5, 914, 1966.
3. Shevelev, I.A. and I.P. Levshina. In: *Elektrofiziologiya tsentral'noy nervnoy sistemy* (Electrophysiology of the Central Nervous System) Tbilisi, 1966, p. 327.
4. Granit, R. *Sensory Mechanisms of the Retina*. Oxford University Press, London, 1947.

Institute of Higher Nervous Activity and Neurophysiology,
USSR Academy of Sciences

RECRUITING OF NEURONS OF THE RABBIT SUPERIOR COLLICULI IN RESPONSES

N. V. Dubrovinskaya

Unit activity in the superior colliculi in response to single, paired, and repetitive photic stimuli was studied in waking rabbits by means of an extracellular tungsten microelectrode. Inhibition developed in 69% of units responding to a single flash. During rhythmic stimulation, the neurons differed in their lability. Prolonged rhythmic action is the condition of labilization of these units.

Several workers [1, 4, 6, 7, 8] have described inhibitory processes participating in the formation of cortical unit responses to various stimuli. In most cases inhibition is found as a pause lasting about 100 msec in a unit discharge, immediately after the initial phase of excitation. Experiments [2, 5] have shown that the inhibition influences the formation of cortical unit responses to paired and repetitive stimuli.

/84

Some properties of inhibitory processes at the level of the superior colliculi, the subcortical center of the rabbit visual system, are described below.

METHOD

Chronic experiments were performed on unanesthetized animals. By means of a hydraulic micromanipulator with remote control a tungsten electrode ($2-5\mu$, $6-7\Omega$) was inserted into the superior colliculi. Single unit activity was recorded extracellularly by this electrode. Single, paired (interval 20-40 msec), and repetitive (1-50 Hz) photic stimuli, at an intensity of 5.21 m/sec, were applied. The derived potentials were fed into a cathode follower and 4-UNCh-4S amplifier and photographed from a Cathode-ray oscilloscope screen on moving film. The location of the electrode tip was determined morphologically by the coagulation method.

EXPERIMENTAL RESULTS

Assessment of unit responses of the superior colliculi to single flashes showed depression of background activity, one of the manifestations of inhibition,

in the response of 69% of reacting units. The latent period and duration of inhibition varied considerably. As an example let us examine two neurons: No. 60, with an inhibitory-excitatory (1a) and No. 10, with excitatory-inhibitory (Fig. 1b) types of response to single flashes. In both cases the duration of inhibition was about 500 msec. Application of repetitive photic stimuli (RPS) to these neurons revealed two distinctive features of their responses: low lability and the possibility of recruiting into the response.

1. Low Lability. An RPS-driving response was observed only during application of the lowest frequencies of the tested range. At a frequency of 2.5 Hz, the probability of a response* by neuron No. 10 falls to 0.4, while application of flashes at 6 Hz causes total suppression of the response in the course of the 7 sec of action of stimulus. Comparison of graphs showing probability of a response by different types of neurons as a function of RPS with the temporal parameters of their excitatory and inhibitory phases shows that the decrease in probability of the response in all cases is due to the fact that successive stimuli begin to reach the neuron toward the inhibitory phase in its discharge. Hence it follows that inhibition significantly influences the formation of the frequency-specific response, actively depressing it.

/87

/85

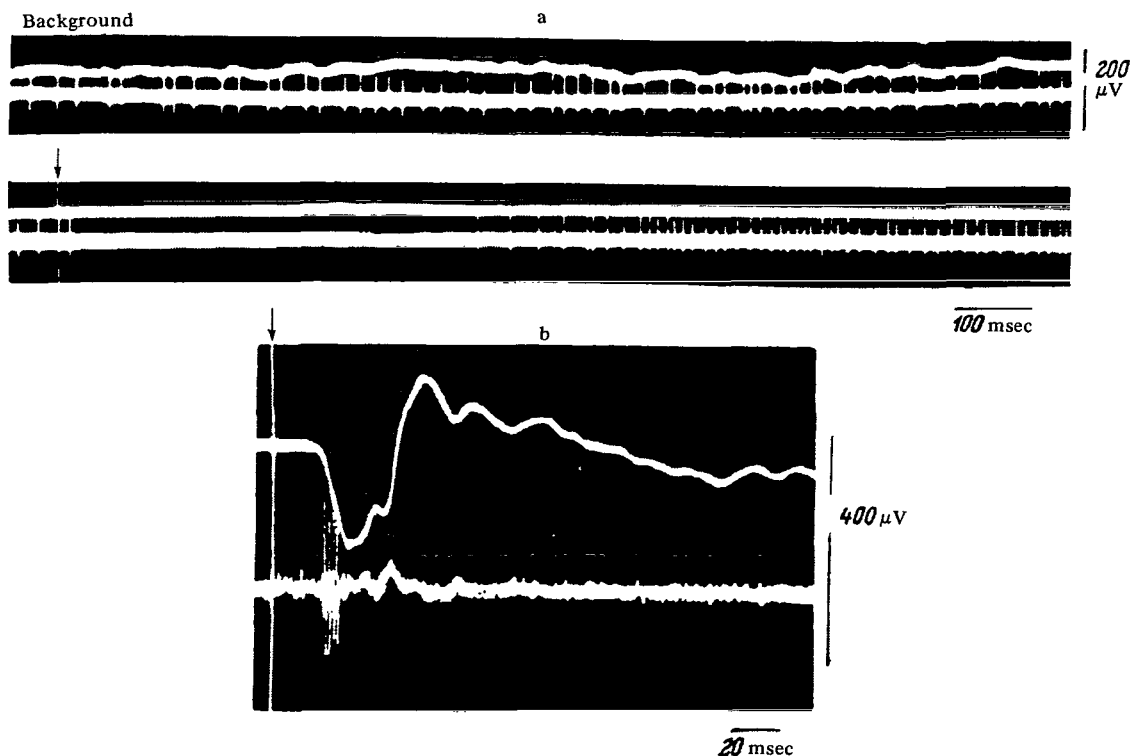


Figure 1. Responses of Neurons No. 60 (a) and No. 10 (b) to a Single Flash. Presentation of Stimulus Shown by Arrow. Upper Curve Denotes Slow Activity, Lower Curve Unit Discharges. Downward Deviation of CRO Beam from Isoelectric Line Corresponds to Positivity.

*The ratio of the number of flashes evoking at least one spike to the total number of flashes in the series.

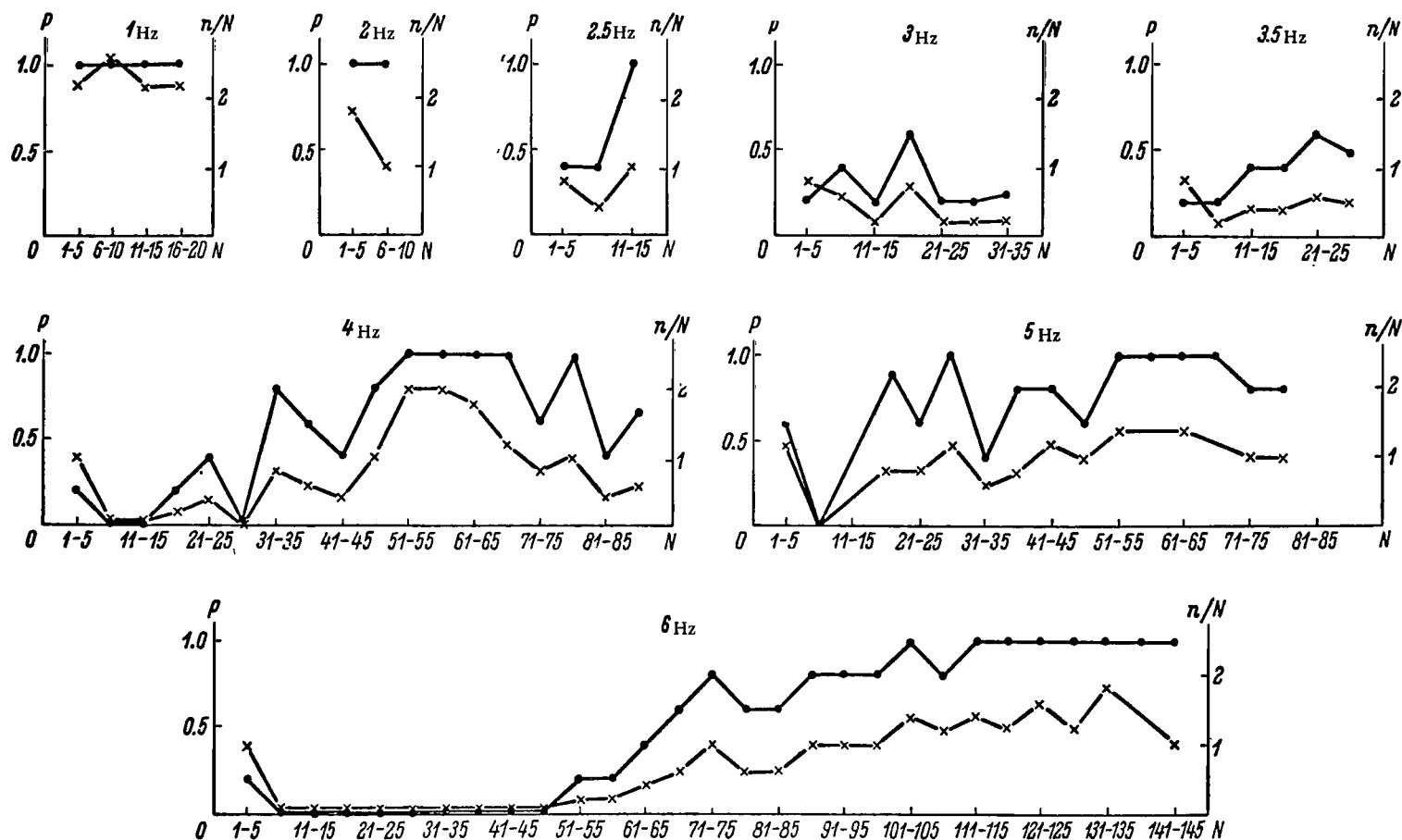


Figure 2. Probability of Response (Points, Left Ordinate) and Ratio of Total Number of Spikes (n) to Number of Flashes Presented (N) (Crosses, Right Ordinate) as Functions of Number of Presentations of Flashes in Series. Frequency of RPS (Hz) Shown above Each Curve. Neuron No. 10.

The mechanism of suppression can be explained by examining the response of neuron No. 60 to paired flashes at different intervals (Fig. 3). If the test stimulus occurs during the inhibitory pause, this produces delay in the second phase of the response, due in all probability to strengthening and accumulation of inhibition.

It can thus be concluded that as a result of summation of inhibition the probability of a response to subsequent stimuli falls considerably, evidence of the low lability of the tested units.

2. Possibility of Recruiting into the Response. During prolonged (10-20 sec) application on RPS a gradual improvement in the response takes place (4-6 Hz) to such an extent (Fig. 2) that each flash in the series begins to produce an effect ($P = 1$). This can be seen especially clearly by the use of flashes at 6 Hz. Despite the absence of response, at the beginning of stimulation its complete restoration is observed starting from the 111th flash in the series. The same phenomenon in neuron No. 60 is shown in Fig. 4. On the left of the histograms the location of this "breakthrough of the inhibitory front" can be seen.

DISCUSSION

A distinguishing property of some neurons of the superior colliculi with an inhibitory pause during the action of flashes is recruiting into the response under the influence of prolonged RPS. This leads to a sharp increase in their lability. A phenomenon of this type has been described in the visual system by Makarov [3] and called labilization. The phenomenon described in this paper can evidently be regarded as labilization at the single unit level. What is its mechanism? The results described show that suppression of the response is connected after the development of active inhibition at the neuronal level, and for this reason it is only with the disappearance of inhibition that the neuron can begin to discharge. Evidently the following system of neurons must be involved in this process: first, the main neuron whose activity is being recorded; second, the neuron inhibiting it and producing the inhibitory pause in the response; and third, an inhibitory neuron of the second order, involved in the activity as the result of prolonged RPS and producing "inhibition of inhibition" and, as a result, recruiting of the main neuron into the response. The possibility of such a mechanism is indicated by the data of Wilson [10] obtained on the spinal cord of cats, when inhibition of interneurons with simultaneous facilitation of the main neuron were observed during intracellular derivation.

/88

/89

The presence of "inhibition of inhibition" has also been demonstrated by Hartline and Ratliff [9] in the eye of the horseshoe crab.

One of the mechanisms of labilization may thus be the disinhibition of the unit response.

Two hypotheses, confirming afferent and efferent functions of the superior colliculi, can be put forward to explain the functional importance of the phenomenon described above: 1) an increase in the efficiency of transmission of information to higher centers, and 2) participation in the formation of the response of tracking a rapidly moving object.



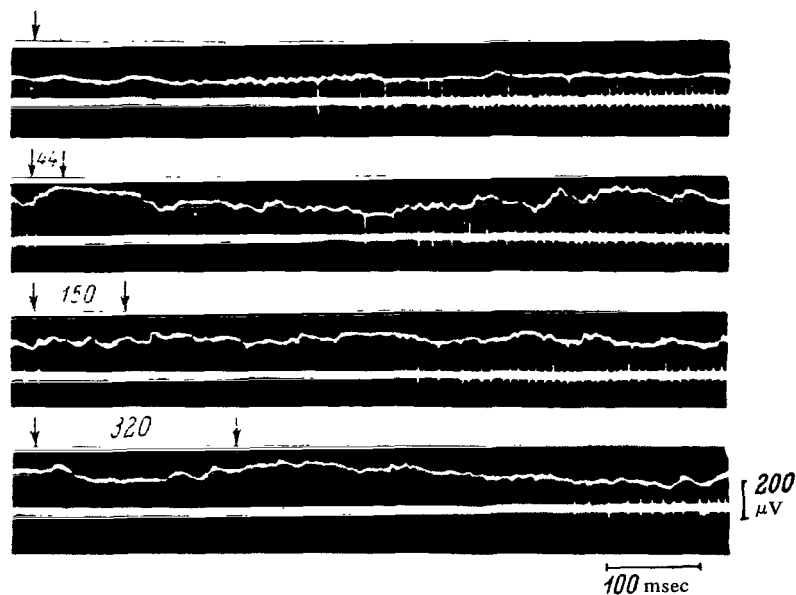


Figure 3. Effect of Presentation of Paired Flashes at Different Intervals (Numbers above Curves). Neuron No. 60. Remainder of Legend as in Fig. 1.

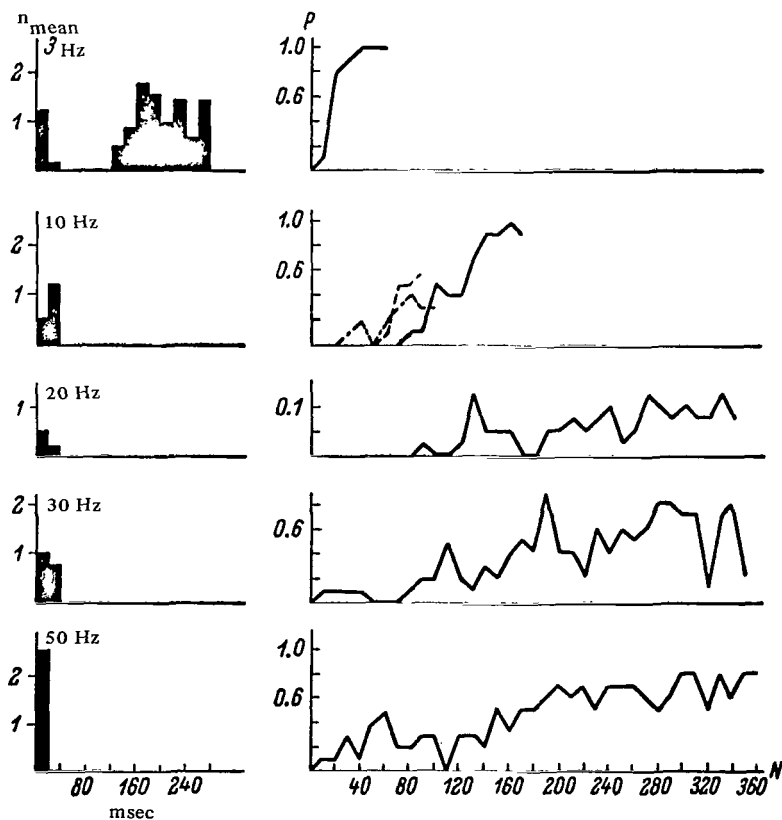


Figure 4. Characteristics of Neuron No. 60 for Different Frequencies of RPS. On the Left: Poststimulation Histograms of Unit Response to Different Frequencies of RPS (Shown by Figures), on the Right: Probability of Response (P) as a Function of Number of Presentations of Flashes in Series for the Same Frequencies (N).

CONCLUSIONS

1. Neurons of the superior colliculi with phased responses to flashes of light including a long period of inhibition show low lability during the action of RPS.
2. Suppression of the response is based on the summation of inhibition.
3. A condition for the labilization of neurons of this type is the prolonged action of RPS, leading to disinhibition of unit responses.

REFERENCES

1. Kondrat'yeva, I.N. Zh. Vyssh. Nervn. Deyat. (Journal of Higher Nervous Activity) 14, 6, 1069, 1964.
2. Kondrat'yeva, I.N. and B.I. Volodin. Zh. Vyssh. Nervn. Deyat. (Journal of Higher Nervous Activity) 16, 5, 874, 1966.
3. Makarov, P.O. Neyrodinamiko zritel'noy sistemy cheloveka (Neurodynamics of the Human Visual System) Leningrad, 1952.
4. Polyanskiy, V.B. Zh. Vyssh. Nervn. Deyat. (Journal of Higher Nervous Activity) 15, 5, 903, 1965.
5. Polyanskiy, V.B. Zh. Vyssh. Nervn. Deyat. (Journal of Higher Nervous Activity) 16, 2, 298, 1966.
6. Skrebitskiy, V.G. and L.L. Voronin. Zh. Vyssh. Nervn. Deyat. (Journal of Higher Nervous Activity) 16, 5, 864, 1966.
7. Andersen, P. and J.C. Eccles. Nature, 196, 645, 1962.
8. Choh-Luhli and S.N. Chau. J. Cell. Comp. Physiol. 60, 1, 1962.
9. Hartline, H.K. and F. Ratliff. J. Gen. Physiol. 40, 357, 1957.
10. Wilson, V.I. and P. R. Burgess. J. Neurophysiol. 25, 392, 1962.

M.V. Lomonosov
Moscow State University



INFLUENCE OF PROLONGED PHOTIC AND ACOUSTIC STIMULI ON UNIT ACTIVITY IN THE LATERAL GENICULATE BODY OF RABBITS

T. G. Beteleva

Using tungsten microelectrodes, the activity of 11 units of the lateral geniculate body was studied in waking rabbits during exposure to flashes at 80 Hz and clicks at 15-95 Hz. The duration of repetitive stimulation and of the intervals between stimuli was 5 min. In six of the eleven neurons this stimulation produced a lasting change in spontaneous activity, either an increase or decrease in its frequency, which the writer interprets as a tonic change in unit activity of the Lateral Geniculate Body.

Light plays an important role in the activating effect of stimulation on cortical tone. The level of conditioned and unconditioned reflexes is increased in light and decreased in darkness [3, 4]. The decisive role of the arrival of impulses along the specific visual pathways for the maintenance of cortical rhythmic activity was demonstrated by the experiments of Novikova et al. [5, 6]. In these experiments, operative or functional exclusion of vision caused a decrease in electrical activity of all parts of the cortex, despite the presence of exaltation in the reticular formation of the brain stem.

The activating action of light has been detected at all levels of the visual system: it has been demonstrated on the ERG and for evoked potentials in the optic tract [9, 10], where activation was manifested mainly as a decrease in the time of development of responses to single stimuli. Illumination of the retina strengthened the postsynaptic components of the response of the lateral geniculate body (LGB) to stimulation of the optic tract [19]. The activating effect of light at the LGB level has also been shown by analysis of the spontaneous activity of this structure [13]. Activation of evoked potentials in the visual cortex by photic stimulation has been described by Chang [12], and Dumont and Dell [15]. There is also evidence of the inhibitory effect of light [11, 23].

To make a fuller study of the character of the effect of photic stimuli, the tonic component of their action in single unit responses can be isolated. In the investigation described below such an analysis was carried out for unit responses of the LGB.

METHOD

Experiments were carried out on unanesthetized rabbits fixed to a frame during the experiments. Activity of LGB neurons was derived by means of tungsten microelectrodes with an impedance of 6-10 M Ω . The microelectrode was inserted into the brain with the aid of a hydraulic micromanipulator, the plastic base of which was fixed to the rabbit's skull.

The stimuli consisted of flashes (80 Hz), replacing a steady light, and clicks of 15-45 Hz. The duration of action of the repetitive photic and acoustic stimuli was 5 min. Periods of photic and acoustic stimulation were separated by dark intervals of 5 min during which the unit activity continued to be recorded.

During analysis of the results the dynamics of changes in the firing rate of the neurons was investigated in darkness and during exposure to photic and acoustic stimuli. An analysis of this type was undertaken for eleven neurons in an intact rabbit and six neurons in a rabbit after enucleation of the contralateral eye.

EXPERIMENTAL RESULTS

/91

In darkness, spontaneous unit activity of the rabbits LGB varies considerably. The slowest frequency of spontaneous unit activity was 4-5 spikes/sec and the highest frequency about 55/sec. Most neurons discharged in darkness at a frequency of 10-15 spikes/sec.

In the intact rabbit prolonged photic stimulation at high frequency evoked a persistent change in the spontaneous activity of six of the eleven tested neurons, which lasted throughout the period of stimulation. In some neurons this change was marked by a decrease (Fig. 1a), and in others by an increase in the discharge frequency (Fig. 1b). The character of the changes depended on the initial level of spontaneous activity. In neurons with a high frequency of spontaneous activity the changes were most commonly inhibitory in character, while if the frequency of spontaneous activity was low, they responded by activation. The use of a long train of acoustic stimuli evoked similar changes in unit activity in the LGB.

The study of dynamics of the firing rate at different times after starting and stopping high-frequency photic and acoustic stimulation showed that the action of the stimuli in darkness in the initial periods evoked a response in some units which differed considerably from the response to the last action of the stimuli. On- and off-effects of stimulation on the firing rate of the neurons which disappeared in the subsequent period of stimulation were regarded as the initial, faster phase of the response. Its duration in different neurons varied from 1 to 5 sec. The presence of a fast on-phase of the response to photic stimulation was recorded in three units, an off-phase in two, and on- and off-phases in three neurons. In some neurons, after the initial phase the level of activity returned to that found in darkness. One such neuron is illustrated in Fig. 2.

/93



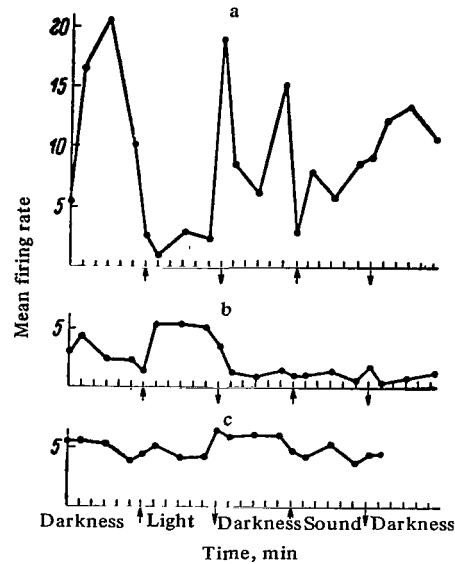


Figure 1. Firing Rate of Neurons in Darkness and During Exposure for 5 Min to High-Frequency Photic and Acoustic Stimuli.

a - Decrease in Firing Rate of Neuron No. 187 during Photic and Acoustic Stimulation; b - Increase in Firing Rate of Neuron No. 198 during Photic Stimulation; c - No Effect of Photic and Acoustic Stimulation on Activity of Neuron No. 230, Increase in Frequency of Activity after Switching off Light. Each Point on Curves is Mean Firing Rate in Separate 5-sec Cuts of the Tracing taken Consecutively 800 msec, 1 min, 3 min, and 5 min after Beginning and End of Stimulation. Times of On and Off Stimulation Shown by Arrows on Abscissa.

If a fast phase occurred in both the on- and off-stages of a unit response to stimulation, the direction of the changes was the same.

A fast phase also developed in the response to acoustic stimuli, but unlike the response to photic stimuli, it was recorded only in the on-response (in 5 units) and never in the off-response. Fast initial phases of tonic changes may be both activating and inhibitory in character and they do not always agree in sign with the subsequent action of the same stimuli.

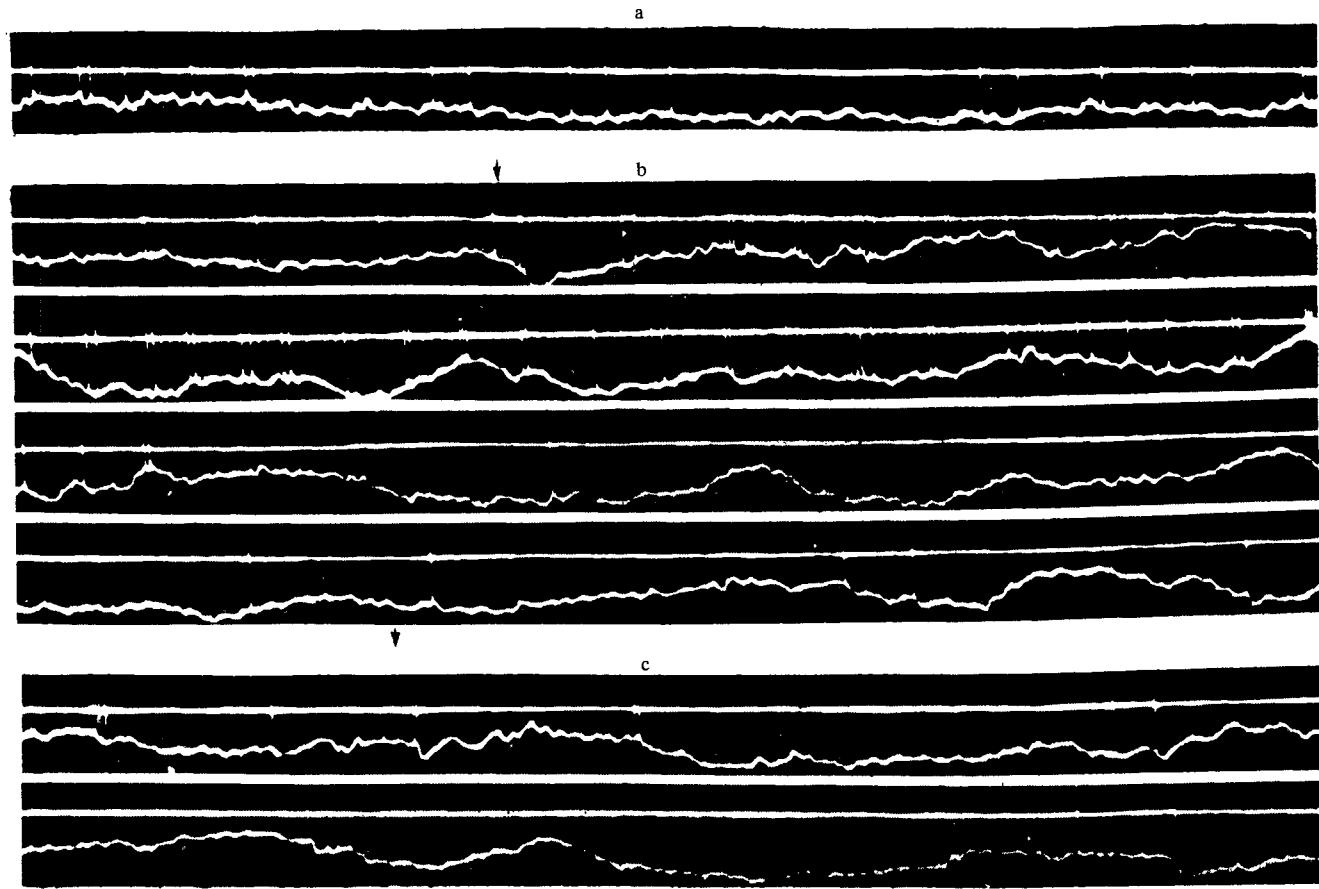


Figure 2. Initial Phase of Change in Activity of Neuron No. 193 during On-Response to High-Frequency Photic Stimulus.

a - Unit Activity in Darkness; b - Unit Activity during Prolonged Photic Stimulation at 80 Hz; c - Unit Response to Single Flash. Curves in b and c are Cuts of a Continuous Tracing. Time of Switching on Photic Stimulus at 80 Hz (b) and Single Flash (c) Marked by Arrows.

The differences between the actions of photic and acoustic stimuli described above were attributed to the fact that the effects of photic stimuli reach neurons of the LGB along two pathways: from the retina and from nonspecific structures. Evidently only the second pathway is possible for acoustic effects. Accordingly, and also bearing in mind that almost complete decussation of the visual fibers takes place in the chiasma, it was postulated that after removal of the contralateral eye relative to the side of recording of the flashes applied to the ipsilateral eye, acoustic stimuli would also begin to evoke the same changes in spontaneous activity.

Experiments undertaken on a rabbit after unilateral enucleation showed that spontaneous activity of neurons of the LGB deprived of its afferent supply is almost indistinguishable from the activity of these neurons in intact animals. Their mean firing rate in darkness was 17.7 spikes/sec. Of six neurons tested five did not respond to flashes applied to the ipsilateral eye.

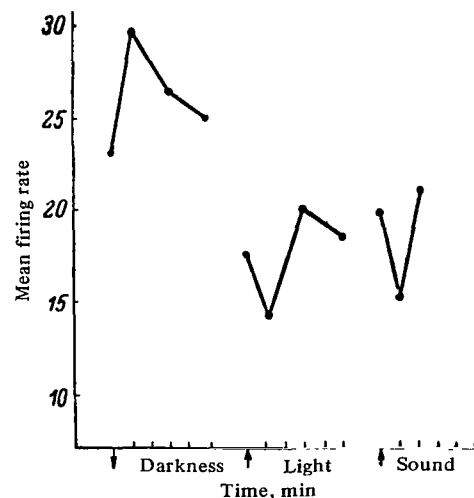


Figure 3. Firing Rate of Neurons No. 158 during Exposure to High-Frequency Photic and Acoustic Stimuli in a Rabbit after Enucleation of the Contralateral Eye. Legend as in Fig. 1.

Application of long series of flashes and flicks to a rabbit after enucleation of the contralateral eye confirmed our hypothesis that the effects of photic and acoustic stimuli would be more similar. However, the character of this effect was found to differ considerably from that observed in intact rabbits. The main difference was in disappearance of the fast initial phases of tonic changes in the firing rate. The tonic changes in unit activity themselves were less marked in the enucleated rabbits, and in all cases tested they were inhibitory in character. The dynamics of changes in the firing rate of a neuron in a rabbit after unilateral enucleation is illustrated in Fig. 3.

The results thus show that application of prolonged photic and acoustic stimuli leads to tonic changes in the activity some LGB neurons, and these changes are associated to some extent with changes at the retinal level.

DISCUSSION

The results of these experiments described above indicate the existence of a tonic component in the action of light on some LGB neurons. It may be asked whether this tonic response develops in the structures of the visual system itself, or whether it is a reflection of the influence of other structures. The results described above do not permit the identification of the place where this response develops. However, the existence of changes in LGB unit activity in the same direction as both on- and off-responses to prolonged photic stimulation, and the coincidence between these changes and those observed in the on-response to a series of acoustic stimuli suggests that tonic responses to light and sound have common mechanisms. This is confirmed by the observations of Dumont and Dell [15] and Sokolov and Dulenکو [10], showing that the effects of specific and nonspecific activation can be summated.

It can be postulated that the tonic effect of photic and acoustic stimuli spreads through one of the nonspecific structures (for example, through the reticular formation of the brain stem). A tonic response accompanying the phasic response to stimulation of the sciatic nerve and to direct electrical stimulation of the reticular formation [17] has been described for neurons of the reticular formation itself. The fact that these responses of the visual system are dependent on the level of waking [14, 18, 23] is evidence of the existence of a tonic influence on this system from the reticular formation. Another source of tonic influences of light on the visual system may be the hypothalamus, which receives optic fibers [2, 8]. Stimulation of the hypothalamus can influence responses of the visual system [7]. However, participation of nonspecific structures in the formation of tonic responses to light has been inadequately studied.

So far as the point of application of tonic influences to the visual system is concerned, experiments in which unit activity was recorded after enucleation of the contralateral eye suggest that changes in activity at the retinal level participate in the formation of tonic responses. This suggestion is also confirmed by the observations on Arden and Söderberg [1], who found that in ischemia of the retina the effects of action of acoustic stimuli on the LGB neurons may be distorted. The influence of nonspecific structures responsible for tonic responses is evidently exhibited at all levels of the visual system.

Several hypotheses have been put forward to explain the mechanisms of photic activation. Some workers [10, 20] consider that the mechanism of strengthening of visual responses during photic stimulation is similar to that of posttetanic potentiation. However, in the synapses of the LGB of unanesthetized animals, tetanization is known to produce depression, and sometimes complete disappearance of the postsynaptic components of the response [15, 21]. The only condition for the development of posttetanic potentiation in the LGB is secondary depression from preliminary tetanization after the use of Nembutal [21]. On the basis of these results it seems most unlikely that posttetanic potentiation can be

the mechanism of specific activation at the LGB level. These mechanisms require further study.

CONCLUSIONS

/95

1. Prolonged photic and acoustic stimuli evoke tonic changes in the activity of LGB neurons which can take the form of either an increase or a decrease in the level of unit activity.
2. An initial fast phase and subsequent phase of persistent change in activity can be distinguished in the tonic responses of the LGB neurons.
3. The formation of tonic unit responses in the LGB to photic and acoustic stimulation is connected with changes at the retinal level.

REFERENCES

1. Arden, J. and U. Söderberg. In: *Teoriya svyazi v senzornykh sistemakh* (Theory of Communication in Sensory Systems), Mir Press, Moscow, 1964, p. 355.
2. Biryuchkov, Yu. V. *Byull. Eksperim. Biol. i Med.* (Bulletin of Experimental Biology and Medicine) 59, 111, 1965.
3. Denisov, P. K. and P. S. Kupalov. *Arkh. Biol. Nauk* 38, 689, 1933.
4. Kostenetskaya, N. A. In: *Trudy fiziologicheskoy laboratorii imeni Pavlova* (Proceedings of the Pavlov Physiological Laboratory) 15, Moscow, 1949, p. 138.
5. Novikova, L. A. *Materialy 1-oy nauchnoy konferentsii, posvyashchennyye problemam fiziologii, morfologii i kliniki retikulyarnoy formatsii* (Proceedings of the First Scientific Conference on Physiology, Morphology, and Clinical Aspects of the Reticular Formation). Moscow, 1960, p. 87.
6. Novikova, L. A. and V. I. Belyayev. *Zh. Vyssh. Nervn. Deyat.* (Journal of Higher Nervous Activity) 13, 4, 715, 1963.
7. Novokhatskiy, A. S. In: *Fiziologiya i patologiya gipotalamusa* (The Physiology and Pathology of the Hypothalamus). Nauka Press, Moscow, 1965. p. 112.
8. Pines, L. Ya. In: *Rukovodstvo po neyrologii* (Textbook of Neurology) 1, 2, Moscow, 1957, p. 577.
9. Sokolov, Ye. N. In: *Oriyentirovanny refleks i problemy retseptsii v norme i patologii* (The Orienting Reflex and Problems of Reception Under Normal and Pathological Conditions). Moscow, 1964, p. 220.
10. Sokolov, Ye. N. and V. P. Dulenko. In: *Oriyentirovanny refleks i problemy retseptsii v norme i patologii* (The Orienting Reflex and Problems of Reception Under Normal and Pathological Conditions). Moscow, 1964, p. 249.
11. Arduini, A. and A. Cavaggioni. *Arch. Ital. Biol.* 103, 652, 1965.
12. Chang, H. *J. Neurophysiol.* 15, 5, 1952.
13. Dabner, H. and R. Gerard. *J. Neurophysiol.* 2, 142, 1939.
14. Dagnino, N., E. Favale, C. Loeb and M. Manfredi. *J. Neurophysiol.* 28, 443, 1965.

15. Dumont, S. and P. Dell. Electroenceph. Clin. Neurophysiol. 12, 769, 1960.
16. Fentress, J. and R. Doty. Fed. Proc. 25, 573, 1966.
17. Machne, X., I. Calma and H. Magoun. J. Neurophysiol. 18, 547, 1955.
18. Maffei, L. and G. Rizzolatti. Arch. Ital. Biol. 103, 609, 1965.
19. Meneders, M. Verhand. von de Koninkl. Vlaamse Acad. voor Geneeskunde van Belgie, 27, 199, 1965.
20. Meneders, M., J. Bergmans and J. Colle. Arch. Ital. Biol. 104, 163, 1966.
21. Morlock, M. and W. Marshall. Exp. Neurol. 9, 96, 1964.
22. Rosenblum, I. Exp. Neurol. 8, 30, 1963.
23. Walsh, J. and J. Cordean. Exp. Neurol. 10, 80, 1965.

Department of Physiology of Higher Nervous Activity,
Moscow State University

HYPOTHALAMIC POTENTIALS EVOKED BY PHOTIC STIMULATION OF THE RETINA

A.S. Novokhatskiy

Demonstration of presence of direct anatomical couplings between the retina and hypothalamus via centripetal and centrifugal fibers. A study of the light-evoked potentials in various parts of the hypothalamus of 32 rabbits tested simultaneously. These evoked potentials were found to have a multicomponent structure and were observed most often in the evoked response from the supraoptic, periventricular, and mamillary nuclei. The evoked response with the maximum amplitude was recorded from the mamillary nucleus. Evoked responses from the dorso-medial and ventromedial nuclei occurred very rarely. Comparison of the latencies of the Electroretinography and evoked responses in the hypothalamus showed that the latency of the anterior nuclei of the hypothalamus often coincides with that of the ERG, while in the mamillary nucleus it averages 10 msec greater, and in the posterior portion it is somewhat shorter.

The higher cortical centers of the visual system (their morphology, physiology, and pathology) have been investigated in more detail than the subcortical centers (lateral geniculate body, pulvinar, superior colliculi). As regards the existence of anatomical connections between the retina and hypothalamus, even today some of the world's leading neurohistologists (Bergman [6], Szentagothai et al. [14]) in general deny it. The main reason is the considerable difficulties encountered in investigating this region. For example, the results of Frey's [10] work, covering a period of 20 years, on the retino-hypothalamic connections proved to be wrong, and the isolated optico-hypothalamic bundle and the medial optic nucleus which he described in fact do not exist. Yet Frey's results had become classical and are cited in many monographs (Markelov [2], Clara [7], Sager [1]).

/96

The work of Knoche [11] began to appear in print in 1965. He completely rejected the results of Frey's investigations [10], asserting that the only way in which the retina and hypothalamus are connected is through the retino-hypothalamic bundle, which he himself discovered. Knoche emphasizes that the fibers of this bundle run in isolation to the hypothalamus, in the substance of the lamina limitans.

The writer has concluded after many years of research [3; 4, 5] that it is illogical to look for an isolated bundle of nerve fibers running from the retina to the hypothalamus. I share the views of the French workers Roussy and Mosinger [13] and Dollander [8] that these connections, because of the nature of the topographical anatomical relations between the chiasma and optic tracts, on the one hand, and the hypothalamus on the other, are diffuse in character.

I have demonstrated the existence of direct (retina-hypothalamus) and reciprocal (hypothalamus-retina) connections. The centripetal fibers of this system consist mainly of axons of special ganglion cells of the retina. An experiment was devised to make it possible to isolate the retino-hypothalamic fibers from the whole mass of optic fibers. Most of these fibers terminate in neurosecretory cells of the anterior hypothalamus, mainly in cells of the supra-optic nucleus (its medial-dorsal-anterior parts), and also in cells of the paraventricular zone (oral areas). A very few descend from the upper surface of the chiasma, posteriorly to Meinert's commissure, in the substance of the tuber cinereum. Only a few of these fibers run further in a caudal direction, and most probably terminate in cells of the anterior part of the reticular formation. The centrifugal fibers of this system also run mainly from cells of the supraoptic nucleus. The number of retino-hypothalamic fibers is small compared with the total number of nerve fibers of the optic nerve. It is through this system that light exerts its influence on the hypothalamus, and the hypothalamus exerts its influence on some functions of the retina. A diagram of the retino-hypothalamic connection is given in Fig. 1.

/97

The great influence of light on regulation of functions of the hypothalamo-hypophyseal system, so far as the formation of biological rhythms and the production of gonadotropic and melanophore hormones are concerned, is well known. On the other hand, personal observations and experimental and clinical data show that the hypothalamus regulates the pressure in the blood vessels of the retina, its electric potential, and its dark adaptation.

According to my investigations this system has not become vestigial in the process of phylogenesis (rabbit, cat, dog, man) but, on the contrary, it has acquired more distinct forms in man.

Because of the peculiarities of its neurosecretory cells, influences of the hypothalamus on the retina are perhaps mediated through neuro-humoral mechanisms. Massopust and Daigle [12], in chronic experiments on cats, obtained an evoked potential from nuclei of the anterior and posterior hypothalamus during photic stimulation of the retina. The latent period of the evoked potential of the hypothalamus averaged 10 msec, while that of the posterior hypothalamus was considerably longer, about 30 msec.

Feldman [9], in acute experiments on cats, also observed a hypothalamic potential evoked by illumination of the retina. The evoked potential from nuclei of the anterior hypothalamus (supraoptic nucleus of the thalamus) had a greater amplitude and shorter latent period, of the order of 8-10 msec. The latent period of the evoked potential recorded from the mamillary nuclei was 30-40 msec, and the amplitude of this potential was much smaller than that recorded from nuclei of the anterior hypothalamus.

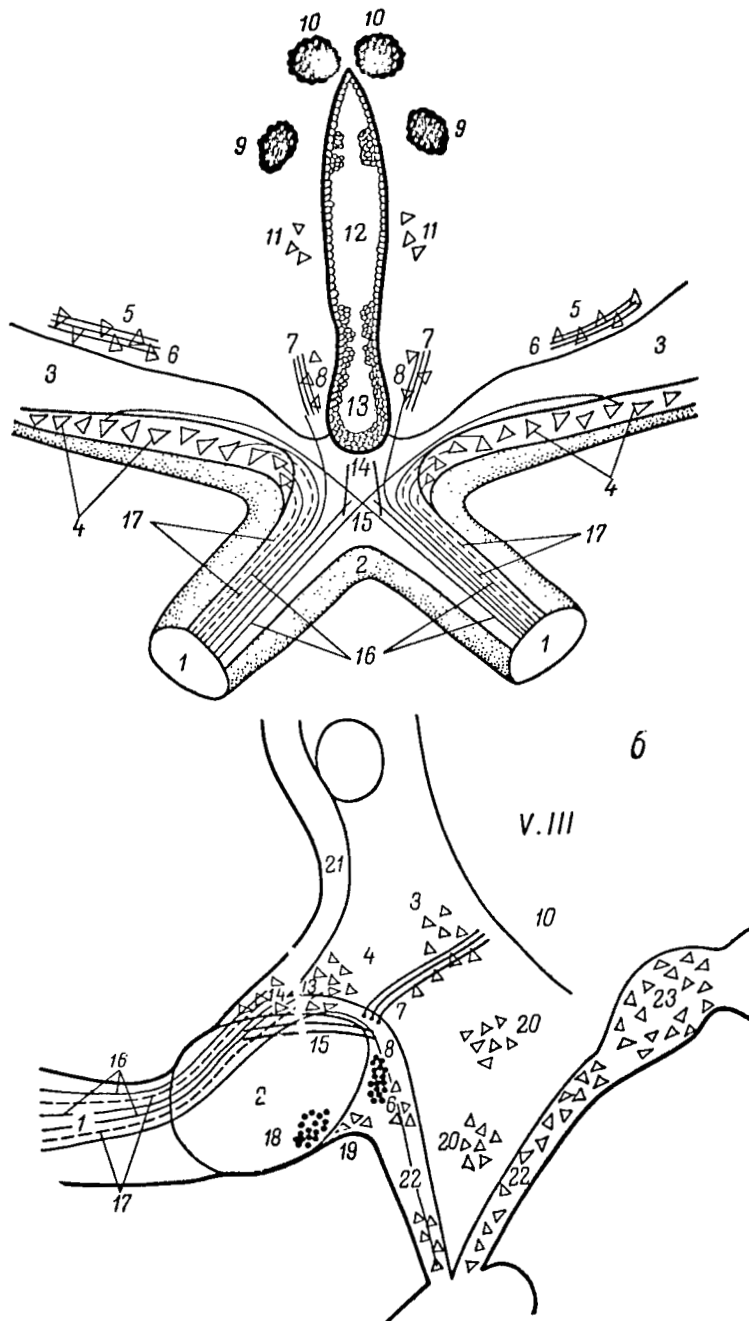


Figure 1. Diagram of Retino-Hypothalamic Connections.
(Caption at top of next page)

(Caption for Fig. 1). a - Oblique-Horizontal Section; b - Sagittal Connection. 1 - Optic Nerve; 2 - Chiasma; 3 - Optic Tracts; 4 - Supraoptic Nucleus; 5 - Posterior Part of Supraoptic Nucleus; 6 - Meinert's Commissure; 7 - Ganser's Commissure; 8 - Paraventricular Nuclear Zone; 9 - Crus Fornicis; 10 - Bundle of Vicq d'Azyr; 11 - Superior Part of Dorsomedial Nucleus; 12 - 3rd Ventricle; 13 - Supraoptic Pouch; 14 - Nuclear Region in Anterior Wall of Supraoptic Pouch; 15 - Bundle of Rothig; 16 - Centripetal Part of Retino-Hypothalamic Tract; 17 - Centrifugal Part of Retino-Hypothalamic Tract; 18 - Gudden's Commissure; 19 - Diffuse Supraoptic Nucleus; 20 - Medial Nuclei; 21 - Lamina Limitans; 22 - Thalamic Nuclei; 23 - Mamillary Nuclei; 24 - Pituitary; V.III) 3rd Ventricle.

In 1962-1963 I carried out experiments on 32 rabbits. Electrodes were introduced into the anterior, middle, and posterior parts of the hypothalamus. Several electrodes were implanted in most rabbits. In several rabbits, electrodes were introduced into the anterior divisions of the reticular formation. The electrodes were introduced by means of a stereotaxic apparatus, and their location was subsequently verified morphologically. The potentials were recorded on a type EEChS-1 2-channel encephalograph with time marker.

Analysis of recordings of the ERG and EEG revealed in most cases a distinct hypothalamic evoked potential in response to illumination of the retina, against the background of slow waves (of the theta- and delta rhythm type). It has a multicomponent structure: a negative is first recorded, followed by a positive wave and a second negative of high amplitude (Fig. 2). The character of the evoked potential, its amplitude, latent period, clarity, and regularity of appearance, were largely determined by the hypothalamic nucleus into which the electrode was implanted.

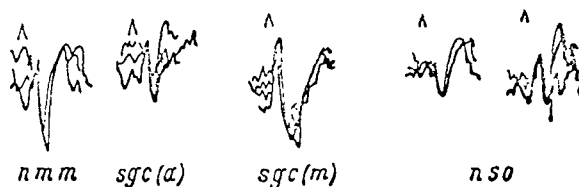


Figure 2. Evoked Potentials in Hypothalamus Obtained by the Reposition Method.

nmm - Medial Mamillary Nucleus; sgc(a) - Substantia Grisea Centralis (Anterior); sgc(m)-Substantia Grisea Centralis (Medial); nso - Supraoptic Nucleus (Two Types of Response).

The evoked potential of clearest amplitude was recorded from the supraoptic (Fig. 3a) and mamillary nuclei (Fig. 3b); in both the first and second cases the amplitude of the waves reached 60-70 mV. The amplitude from the supraoptic diffuse and paraventricular nuclei varied around 30 mV. Very rarely an evoked potential could be recorded from the dorsomedial and ventromedial nuclei. The amplitude was very variable, even during the same experiment.

Most commonly the evoked potential had three components in its structure, but sometimes (especially in the case of evoked potential of the supraoptic nucleus) it consisted of only two components: a small negative wave and large positive wave. The second negative wave was not recorded.

It was not always possible to obtain an evoked potential from nuclei of the hypothalamus in response to every flash (frequently 1-2 Hz).

A potential, evoked by light, was also recorded from the anterior nuclei of the reticular formation (substantia grisea centralis at the level of the anterior parts of the aqueduct of Sylvius, Fig. 3c).

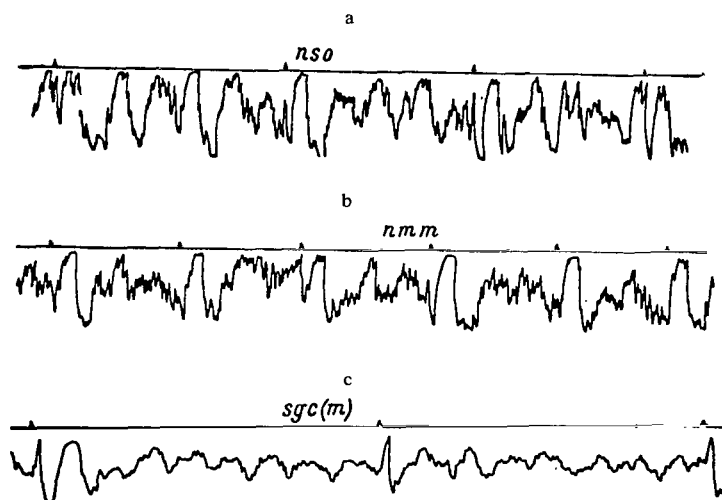


Figure 3. Hypothalamic Evoked Potentials.

a - From Supraoptic Nucleus; b - From Medial Mamillary Nucleus; c - From Substantia Grisea Centralis (Medial Part). Top Line is Marker of Stimulation. Remainder of Legend as in Fig. 2.

Latent periods of the ERG and of the hypothalamic potential evoked by light were as follows.

The retinal latent period varied from 8-25 msec, most commonly 14-15 msec. The latent period of the hypothalamic response varied, but between much narrower limits than the retinal time. The latent period of the anterior nuclei was 14-20 msec, and it frequently coincided in time with the retinal latency, and for that reason the difference between these indices was 0-5 msec. The mean latent period of the evoked potential of the mamillary nucleus was 28 msec, but in some cases it reached 40 msec. The time from retina to posterior hypothalamus was 10 ± 4 msec. The existence of a potential, evoked by photic stimulation of the retina, in nuclei of the anterior hypothalamus (supraoptic and diffuse supraoptic) can be understood because morphological investigations by other workers and myself have demonstrated the presence of direct retino-hypothalamic connections.

The appearance of a well-marked evoked potential in the mamillary nucleus in response to photic stimulation of the retina was somewhat unexpected. This potential, as my own investigations and those of Massopust and Daigle [12] and Feldman [9] have shown, was recorded constantly and clearly. At the same time, no direct anatomical connections could be found between the retina and mamillary nuclei. No indications of their presence likewise could be found in the literature. It was therefore postulated that an indirect connection, involving an interneuron, exists between the retina and mamillary nuclei.

The hypothesis of the existence of an indirect connection between the retina and mamillary bodies was first expressed by Massopust and Daigle [12] in 1962, and repeated in 1964 by Feldman [9]. The evoked potential which I recorded from the anterior nuclei has a very short latent period; the latent period of the evoked potential of the mamillary nuclei is much longer. The very considerable prolongation of the latent period cannot, of course, be explained by the more caudal (relative to the super optic) position of the mamillary nuclei because this distance is only 4-5 mm. The increased latency can only be explained by delay of the impulse in synapsis. By what hypothetical pathway can impulses from the retina reach the mamillary nuclei? Most probably through the hypothalamus, for in my experiments with bilateral division of the optic tract slightly laterally to the hypothalamus, the evoked potential in the mamillary nuclei to illumination of the retina appeared just as clearly.

CONCLUSIONS

1. An evoked potential to photic stimulation of the retina was recorded in the hypothalamic region from the supraoptic and mamillary nuclei and from the anterior divisions of the reticular formation.
2. In most cases no evoked potential could be obtained from the dorso-medial and ventromedial nuclei in response to illumination of the retina.

REFERENCES

1. Sager, O. The Diencephalon. Bucharest, 1962.
2. Markelov, G.I. Zabolevaniya vegetativnoy nervnoy sistemy (Diseases of the Autonomic Nervous System), Moscow, 1948.
3. Novokhatskiy, A.S. Anatomicheskiye svyazi zritel'nykh putey s gipotalamusom (Anatomical Connections of the Optic Pathways with the Hypothalamus), In: Voprosy neyrooftal'mologii (Problems in Neuroophthalology). Kharkov, 1958.
4. Novokhatskiy, A.S. Materialy nauchnoy konferentsii, posvyashchennyye 90-letiyu so dnya rozhdeniya V.P. Filatova (Proceedings of Scientific Conference to Celebrate V.P. Filatov's 90th Birthday), Odessa, 1965, p. 34.
5. Novokhatskiy, A.S. In: Fiziologiya i patologiya gipotalamusa (Physiology and Pathology of the Hypothalamus), Moscow, 1966, p. 112.
6. Bargman, W. Das Zwischenhirn-Hypophysen System (The Midbrain Pituitary System). Berlin, 1954.
7. Clara, M. Das Nervensystem des Menschen (The Nervous System of Man). Leipzig, 1959.
8. Dollander, A. La voie nerveuse opto-tangentielle chez la Cobaye, (The Opto-tangential Nerve Path in the Guinea Pig). Thèse de Nancy, 1947. Abstracted by Magitot, A.A. D'Ocul., 181, 423, 1948. /101
9. Feldman, S. Ann. New York Acad. Sci., 117, 53, 1964.
10. Frey, E. Neue anatomische Ergebnisse zur Phylogenie der Sehfunktion (New Anatomical Data on the Phylogeny of Vision). Augenarzt, 23, 45, 1956.
11. Knoche, H.Z. Mikr. Anat. Forsch. 63, 461, 1967.
12. Massopust, L.C. and H. Daigle. Exp. Neurol., 3, 476, 1962.
13. Roussy, G. and M. Mosinger. Traité de Neuroendocrinologie (A Treatment of Neuroendocrinology), Paris, 1946.
14. Szentagothai, S., B. Flerco, B. Mess, and B. Holasz. Hypothalamic Control of the Anterior Pituitary. Budapest, 1962.

Ukrainian Scientific Research Institute of Eye Diseases
 imeni Professor Girshman

LIGHT-EVOKED POTENTIALS IN HEALTHY PERSONS
AND IN PATIENTS WITH PATHOLOGICAL LESIONS
IN VARIOUS PARTS OF THE VISUAL SYSTEM

Ye. N. Semenovskaya, A. I. Bogoslovskiy,
and V. K. Zhdanov

Data relating to the site, character, and decree of the pathological focus at different levels of the visual system are compared with the results of a combined electrophysiological investigation of the organ of vision (based on evoked potentials and the electroretinogram). Patients with a pathological state of the optic nerve, with various diseases of the retina, with diencephalic disturbances of regulation of the intraocular pressure, and with glaucoma and amblyopia were investigated. It is shown that a careful study of cortical evoked potentials, together with the use of combined electrophysiological methods, can substantially facilitate the determination of the character and location of a lesion in the organ of vision.

Light-evoked potentials in the occipital cortex are a polyphasic response which can be recorded in the electroencephalogram during photic stimulation of the human eye.

/102

There is an extensive literature on evoked potentials in animals and man, methods used to record them and to average and analyze them with the aid of modern computers, the analysis and description of components of the polyphasic cortical response to light, and the schematic representation of its successive temporal phases [1, 3, 5, 14, 15, 17, 18, 20, 22-24, 26-28, 29-31, 33-35]. It was not until 1960-1964 that work was published in which evoked potentials (EPs) were investigated in patients with diseases of the visual system. Papers by Van Balen and Henkes [14, 15, 16], Asafov [1], and Yermolayeva [5] appeared almost simultaneously and independently.

The combined electrophysiological method developed by the writers [10, 12] makes it possible for the first time to determine the location of a pathological lesion in the organ of vision. The object of this investigation was to demonstrate how this method can provide an approach to the elucidation of the cause of a disturbance or absence of the EP in relation to the location, character, and decree of a pathological process at different levels of the visual system.

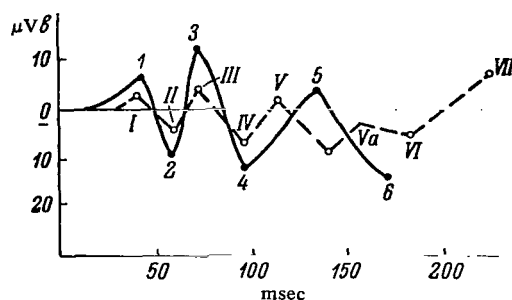


Figure 1. Components of the Evoked Potential.

Abscissa, Time, msec; Ordinate, Amplitude, μ V. Continuous Line Shows Arithmetic Mean of 20 Responses to Photic Stimulation Obtained Near the Midline in the Parieto-Occipital Region. I-VII - Peak Values of Evoked Potential, after Ciganek. 1-6 - The Same in Subject B, Aged 63 Years. Remainder of Explanation in Text.

Despite difficulties in the recording and analysis of evoked potentials in man, there is considerable unanimity in the literature regarding the temporal parameters, amplitudes, and certain other properties of EPs.

The scheme proposed by Ciganek [23, 24], which has been confirmed by the writer's own observations was used for these investigations.

By analysis of an extensive statistical material, Ciganek obtained the following temporal indices for light-evoked potentials in the occipital cortex in man. Latent period 25-28 msec. To 1st surface-positive peak 30-40 msec, amplitude 1-5 μ V. To 2nd surface-negative peak 45-55 msec, amplitude 2-7 μ V. To 3rd surface-positive peak 65-76 msec, amplitude 3-10 μ V.

/103

These three maxima are taken as primary responses of the visual cortex, and the second and third peaks are particularly stable and significant; the first peak sometimes cannot be detected.

These are followed by secondary peaks of the evoked potential: the fourth negative peak, arising 94-100 msec after the flash, and later peaks up to 200-300 msec.

They are called secondary because they evidently are not connected with the arrival of excitation in the visual cortex along specific visual pathways, but are the result of the conduction of excitation along nonspecific pathways.

The secondary response is under the influence of the reticular formation and of drugs acting on it (largactil) [chlorpromazine], which is not true of the primary peaks: they are more resistant. The EP shown in Fig. 1 was obtained by calculating mean values for one subject on the basis of Ciganek's scheme, and it illustrates the close temporal correlation between the subject's primary response and the scheme.

Voghan and Katzman [34, 35] investigated healthy persons and found that peak I is absent in one-third of persons, peak III is always visible, and II is visible in 97% of persons. The absence or modification of peak II is considered to be a most reliable indicator of pathological processes.

Van Balen and Henkes [15, 16] distinguish an effect of attention which, according to their findings, shortens peak I of the response (C_1), while peak II (C_2) develops approximately 100 msec after the flash. In amblyopes and in patients with strabismus C_1 is absent; these workers call this phenomenon "vision without attention." In achromats C_1 does not appear because of the absence of cone vision, and C_1 is therefore associated with central cone vision.

MATERIAL

Altogether 85 patients with pathological lesions in different situations were investigated. The location of the lesion was shown by the character of changes in the evoked potentials and also by the results of clinical and combined electrophysiological methods of investigation of the organ of vision.

The categories of patients were as follows: atrophy, neuritis, and discontinuity of the optic nerve — 10 patients, diseases of the macula 12, retinitis pigmentosa 2, detachment of the retina 8, occlusion of the central artery of the retina 6, total achromatopsia 2, glaucoma 10, combined glaucoma and cyclitis 3, diencephalic insufficiency with raised intraocular pressure 21, amblyopia 8, hypertensive fundus oculi 1, malignant adrenal tumor (pheochromocytoma) 1, benign adrenal tumor 1.

METHOD OF RECORDING EVOKED POTENTIALS

To record the EPs, a standard VEKS-1 vectorcardiograph and an Alvar REEGA-15 electroencephalograph were used. The recording electrodes were connected to the input of one channel of the electroencephalograph, and a cathode follower was connected to the output of the second amplification cascade. The input of the VEKS instrument was connected to the output of the cathode follower. Voltage to the input of the VEKS was fed through a symmetrical voltage divider with grounded mid point, which considerably reduced the induction level. The horizontal sweep of the VEKS instrument was synchronized with flashes from an "Alvar" photophonostimulator, with a flash energy of 0.3 J and duration 50 μ sec. Synchronization of the sweep of the VEKS instrument with the flashes was achieved as follows: the horizontal sweep and action of the photostimulator were triggered by two pairs of contacts of an RSI relay.

The instrument made it possible to record potentials before photic stimulation by retarding the flash. The potentials were photographed from the CRO screen by means of a Smena-2 camera.

The various methods used for the combined electrophysiological investigations were described previously [10, 12].

EXPERIMENTAL RESULTS

Evoked potentials and electrophysiological indices of patients with pathological lesions of the optic nerve (neuritis, atrophy, or discontinuity of the optic nerve).

Patient Sh., a man aged 34 years, was examined on October 23, 1965 (out-patient no. 40044) and had a complete discontinuity of the optic nerve resulting from injury. Patient S., a young man aged 19 years, had left optic atrophy following trauma. He was examined on April 23, 1964 (out-patient no. 24670). The results of examination of these patients are shown in Table 1.

/104

TABLE 1.

Visual acuity		Phosphene (threshold, μA)		Lability (Hz)		Electroretinogram				EP during photic stimulation	
						Amplitude of wave b (μV)		Frequency of reproduced rhythm, Hz		R	L
R	L	R	L	R	L	R	L	R	L		

Patient Sh.

0 | 0 | Abs. | Abs. | - | - | 175 | 180 | 26 | 26 | Abs. | Abs.

Patient S.

1.0 | 0 | 40 | 800 | 28 | 4 | 350 | 75 | 30 | 24 | Normal | Abs.

Note: R signifies Right Eye, L Left Eye.

The sharp decrease in lability in the left eye will be noted, in agreement with our previous observations demonstrating how this parameter indicates a lesion of the optic nerve. According to the results in Table 1 in patient S. not only the optic nerve, but also the retina was involved in the pathological process; an increase in the threshold of phosphene, a decrease in amplitude of the b wave of the ERG, and some decrease in the frequency of the flashes reproduced by the retina are observed in this case. No potential was evoked by illumination of the left eye.

Patient S., a girl aged 15 years, was examined on February 19, 1966 (case no. 77). Diagnosis: retrobulbar neuritis of the right eye. Visual acuity 0.02, threshold normal (40 μA), lability reduced to 20 Hz (normal about 40).

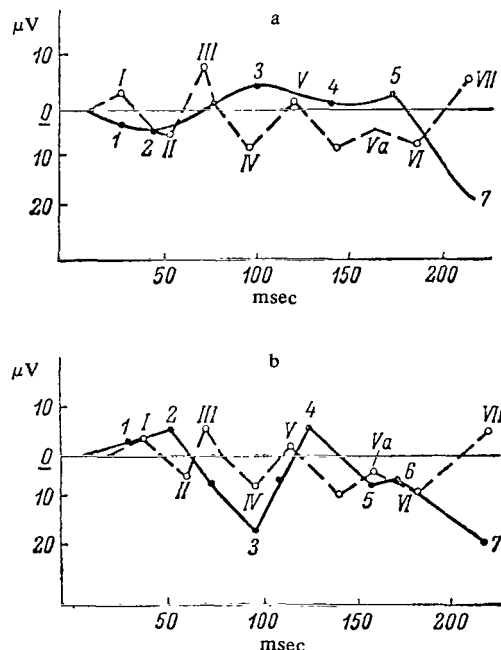


Figure 2. Graph of Mean Values of EP Components.

a - in Patient S., Aged 15 Years, with Retrobulbar Neuritis; b - the Same in Patient T., with Detachment of the Retina. Direction of Peak II is Modified; Peaks III, IV, and VII are Distorted and Delayed. Legend as in Fig. 1.

The configuration of the evoked potential is almost unrecognizable: the direction of peak I is reversed, peak III is delayed, and peak VII is distorted (Fig. 2). Because of the pathological state of the optic pathway, as shown by the reduced lability), the EP is less clearly defined but is not absent, as after discontinuity of the optic nerve or total atrophy. Neuritis gives a more varied pattern on the EP, evidently depending on the number of affected fibers of the optic nerve. The level of lability reflects the severity of the lesion, especially of the axial bundle, and it thus can shed light on the cause of the deviation of the evoked potential from normal.

Yermolayeva [5] observed lengthening of the latent periods of all components of the EP in patients with diseases of the optic nerve. Voytinskiy,

TABLE 2.

Visual acuity	Phosphene (threshold, μA)						Lability, Hz		Electroretinogram				Time of development of consecutive EP peaks (msec)										
	L		R		L		R		L		R		Amplitude of wave b (μV)	Frequency of reproduced rhythm, Hz		I	II	III	IV	V	VI	VII	
														R	L								
R																							
Counting fingers next to face . . .	0.04	140	55	36	40	100	200	20	44	<u>Abs</u> <u>Abs</u>	<u>Abs</u> <u>Abs</u>	<u>Abs</u> <u>Abs</u>	<u>Abs</u> <u>Abs</u>	<u>Abs</u> <u>Abs</u>	<u>Abs</u> <u>Abs</u>	<u>Abs</u> <u>Abs</u>	<u>Abs</u> <u>Abs</u>	<u>Abs</u> <u>Abs</u>	<u>Abs</u> <u>Abs</u>	<u>Abs</u> <u>Abs</u>	<u>225</u> <u>200</u>	<u>300</u> <u>250</u>	

Note: Numerator indicates EP during photic stimulation of right eye, denominator ditto for left eye.

Yermolayeva, and Kharauzov [4] distinguish the two most informative signs, from their point of view, for the EP in diseases of the optic nerve, namely: the peak times of the first and maximal positive deflections, which were chosen by these workers after analysis of their material by a computer.

Evoked potentials in diseases of the retina.
Pathology of the macular region.

In cases of degeneration of the macular region, when the region of central vision is affected at the primary receptor of light, the most characteristic feature revealed by electrophysiological investigation is a decrease in the ability of the retina to reproduce the rhythm of photic stimulation (as shown by the ERG) especially in red light, received by the cones. If the pathological process spreads over a wider area, other signs of reduced function may appear in the organ of vision.

Patient Ya., aged 62 years, was examined on April 29, 1965 (out-patient no. 16404); degeneration of the macular region in the right eye with extensive changes in the fundus oculi, high myopia in both eyes, senile cataract in the left eye. The results of the examination are given in Table 2.

The threshold is increased in the right eye and the amplitude of the b wave of the ERG is lowered. The periphery of the retina is evidently affected by the pathological process also, but the frequency of the rhythm reproduced by the retina is particularly low. The lability index shows that the optic nerve is intact in both right and left eyes. The absence of primary responses during photic stimulation of the right eye in the evoked potentials (I, II, III, and even IV and V) is apparently explained by degeneration of the macular region. In the left eye, where despite the cataract, the retina and its macular region are unaffected (threshold, ERG, and rhythm frequency normal), the EP during photic stimulation gives primary peaks starting with II, after a short delay.

Detachment of the retina is evidently not a local but a systemic disease; it is associated with high myopia. According to the writer's observations [2], it may be accompanied by marked changes in the electroencephalogram, with a very low voltage of the brain potentials and absence of the alpha-rhythm. The EEG in disturbances of distance receptors was the subject of a dissertation by L. A. Novikova [9].

The degree of damage to the retina depends on the size of the detached area, the duration of detachment, as well as on other very important factors. The degree of affection to the retina is reflected in electrophysiological indices in the thresholds and degree of reduction of amplitude of the ERG waves.

In two patients with low visual acuity (down to 0 in one eye) and with high thresholds (up to $600 \mu A$) (sometimes phosphene could not be evoked even at $1000 \mu A$), and in the absence or very low amplitude of the b wave of the ERG, no evoked potential developed. If the patients developed phosphene, the lability could be normal. This meant that the pathway along the optic nerve for photic excitation was free, and the development of the EP was prevented by a lesion of the retina itself.

Patient T., a woman aged 24 years, was examined on April 9, 1965 (case no. 4427) after operation for detachment, high myopia. Visual acuity: recognized correct projection of light. No phosphene develops. Distortion of some components of EP during photic stimulation of eyes (Fig. 2B). This case suggests a parabolic state in the nervous structures of the organ of vision at the retinal level.

Evoked potentials in diencephalic insufficiency and disturbance of regulation of intraocular pressure.

In the patients of this group, in contrast to those described previously, visual acuity and all electrophysiological indices characterizing the retina or optic nerve were normal (except in two patients). However, light-evoked potentials are not typical and are sometimes absent. The defect evidently lies above the optic nerve and tract [3, 7, 8]. Characteristically, delay is frequently found in the development of the EP peaks by comparison with the scheme: the peak in the positive direction has increased amplitude and develops after 150 msec, while the others are absent or reduced. Three patients will serve as examples of the characteristic features.

In the first patient delay in the EP peaks can be associated with the presence of a delta-rhythm, arising presumably from subcortical structures, for it is visible only with monopolar recording; in the second patient the low-voltage character of the EEG and the ill-defined reaction to 0 and 3 can explain the abnormality of the EP. In the third patient lability is reduced, possibly connected with a pathological state not only of the optic nerve, but also of higher levels of the central nervous system, because lability (the critical frequency of phosphene) is determined on the basis of the subject's response. Such a response can be produced only with the participation of the cortex, the functional state of which is

greatly influenced by the diencephalon and reticular formation. Pathology of the diencephalic region (mainly the hypothalamus) in all probability disturbs the normal development of the EP, usually in the direction of slowing it, i.e., a decrease in lability of the responding cells.

Evoked potentials in glaucoma

/107

A numerically identical group of patients with incipient glaucoma (apart from one with almost absolute glaucoma) was chosen for comparison, and just as with the patients with diencephalic insufficiency, their vision was good and their thresholds and ERG normal. In most patients with glaucoma the lability was reduced, corresponding to the writers' early observations on a large number of patients [11, 12]. The object was to compare these two groups by the pattern of their EPs and the character of their EEG. It has been postulated, of course, that glaucoma may be central in its pathogenesis, and that diseases of the diencephalic (hypothalamic) region may play an important role in the etiology of this disease. It is impossible here to discuss the hypothesis, and we shall simply describe some results obtained by the investigation of patients with glaucoma and diencephalic insufficiency [13]. In glaucoma the lability in most cases was reduced and the ERG normal: peaks I and II of the EP were equally frequently absent in both groups. Absence of peak II indicates defects in visual system, despite good visual acuity. Peaks III and IV are rarely absent, but they are delayed and increased in amplitude in patients with diencephalic insufficiency. This may mean that they are greatly under the influence of the pathological diencephalic focus. The subsequent peaks V, VI, and VII are absent more frequently than peaks III and IV.

In the cat *encéphale isolé* preparation, Dumont and Dell [31] found an increase in the secondary peaks during stimulation of the reticular formation, whereas the primary peaks were unchanged. On this basis, these later peaks were regarded as nonspecific relative to the visual system.

The absence of peaks can nevertheless occur in both groups, but in the diencephalic group it is the "secondary" peaks (IV-VII) ascribed to activity of the nonspecific systems, which are frequently absent; this does not conflict with the location of the pathological focus.

In patient B., a woman aged 67 years, with glaucoma of both eyes (out-patient no. 4769), EPs were recorded during photic stimulation. In response to photic stimulation of the better eye, peaks II, III, IV and V appear after some delay, and VI after even greater delay. Photic stimulation of both eyes evoked absence of primary peaks for more than 100 m sec; peak I is visible after 150 msec, and this followed by a group of small peaks, and 380 msec later by a peak of high amplitude. Involvement of the worse eye in the response left its impression on the EP, for the primary peaks disappeared; the ERG is normal.

Evoked potentials in amblyopia

Amblyopia is a disease of unknown etiology and location. Seven patients were investigated. Recordings of the EEG with evoked potentials revealed absence of EP to photic stimulation in five cases, indicating that the higher visual centers may

perhaps be involved in the genesis of amblyopia, because in these patients electrophysiological investigations of the retina and optic nerve gave no reason to suggest a pathological state of these structures, other than in one case when the threshold of phosphene was raised in one eye.

CONCLUSIONS

1. The scheme of temporal development of light-evoked potentials in the electroencephalogram of healthy persons obtained in these investigations coincides with the well-known scheme of Ciganek and several other investigators. Changes in the character of development of the EP in these patients can thus be reasonably ascribed to the action of diseases of the organ of vision localized in various situations.

/108

2. Investigation of the characteristics of evoked potentials in various diseases at different levels of the visual system with verification of the location of pathological lesions by the writers' combined electrophysiological method, with recordings of electrical sensitivity, lability, the ERG, and the background EEG, revealed the probable cause of the abnormality of the EP in each case.

3. A disease of the optic nerve accompanied by a decrease in lability frequently led to the absence or a considerable modification of the EP configuration. The severity of the optic nerve lesion determined the degree of change in the EP.

4. In diseases of the retina, on the side of degeneration of the macular region primary specific peaks and the entire EP were absent in some cases. Many different diseases of the macular region were accompanied by very different patterns of EP.

5. In detachment of the retina, the direction of the peaks was disturbed, the primary components of the EP were absent, but the secondary components still persisted. The severity of the retinal lesion affected the threshold levels of phosphene and the ERG.

6. In patients with diencephalic insufficiency, and also with glaucoma, in the presence of normal visual acuity, threshold, and lability, the primary peaks I and II in the EP were frequently absent and the secondary peaks delayed. Analysis of the background EEG in these patients suggests that abnormalities in the EP are most probably due to the pathological state in the system of diencephalon-cortex, hypothalamus, and reticular formation. The primary peaks (I, II, III) are usually regarded as resistant to influences from the reticular formation; this view is not confirmed by the present investigation: pathology of the diencephalon can lead to their disappearance. New aspects of the genesis of light-evoked potentials thus arise and require discussion.

7. Abnormality of the EP pattern despite integrity of the retina and optic nerve is observed not only during photic stimulation of the amblyopic eye, but also during photic stimulation of the opposite eye in the same patient, thus raising the problem of the role of visual centers in the genesis of amblyopia.

REFERENCES

1. Asafov, B.D. In: *Elektrofiziologicheskiye issledovaniya v klinike ekspertnoy praktike* (Electrophysiological Investigations in Clinical Practice and in Fitness Tests). Meditsina Press, Leningrad, 1964, p. 27.
2. Bogoslovskiy, I.A. and Ye.N. Semenovskaya. *Vestn. Oftal'mol.* (Ophthalmological News) 5, 44, 1960.
3. Brazier, M. In: *Retikulyarnaya formatsiya mozga* (Reticular Formation of the Brain). Medgiz, Moscow, 1962, p. 142.
4. Voytinskiy, S.A., R.Ya. Yermolayeva and K.N. Kharauzov. *Tezisy 5-go soveshchaniya po fiziologicheskoy optike* (Abstract of Proceedings of the Fifth Conference of Physiological Optics). Moscow—Leningrad, 1966, p. 21.
5. Yermolayeva, R.Ya. *Tezisy 5-go soveshchaniya po fiziologicheskoy optike* (Abstract of Proceedings of the Fifth Conference of Physiological Optics). Moscow—Leningrad, 1966, p. 37.
6. Sager, O. *The Diencephalon*. Rumanian Academy of Sciences Press, Bucharest, 1962.
7. Zimkina, A.M. In: *Elektrofiziologicheskiye issledovaniya v klinike i ekspertnoy praktike* (Electrophysiological Investigations in Clinical Practice and Fitness Tests). Meditsina Press, Leningrad, 1964, p. 47.
8. Latash, L.P. In: *Fiziologiya i patologiya dientsefal'noy oblasti golovno mozga* (Physiology and Pathology of the Diencephalic Region of the Brain) USSR Acad. Sci. Press., Moscow, 1963, p. 165.
9. Novikova, L.A. *Elektricheskaya aktivnost' mozga pri narusheniyakh distantnykh retseptorov* (Electrical Activity of the Brain in Disturbances of Distance Receptors). Moscow, 1965.
10. Semenovskaya, Ye.N., A.I. Bogoslovskiy, and G.Ya. Khvoles. In: *Electroretinographia* (Electroretinography), Symposium Luhačovice, 1959, pp. 313-315.
11. Semenovskaya, Ye.N. and L.P. Bakhholdina. In: *Informatsionno-metodicheskiye materialy instituta imeni Gel'mgol'tsa* (Technical Information Reports of the Helmholtz Institute), Moscow, 1956, p. 42.
12. Semenovskaya, Ye.N. *Elektrofiziologicheskiye issledovaniya v oftal'mologii* (Electrophysiological Investigations in Ophthalmology). Medgiz, Moscow, 1963. /109
13. Semenovskaya, Ye.N., A.I. Bogoslovskiy, A.Ya. Vilenkina, L.N. Kozlova, and G.Ya. Chernyavskiy. *Sci. Mem. Helmholtz Inst.*, 7, Moscow, 1965.
14. Van Balen, A.T.M. *De electroencephalographieke reactie op light rickveling en zijiv betvrenis voor de cogheebcundige diagnostick*. Diss., Rotterdam, 1963.
15. Van Balen, A.T.M. and H.B. Henkes. *Brit. J. Ophthalmol.* 44, 449, 1960.
16. Van Balen, A.T.M. and H.B. Henkes. *Brit. J. Ophthalmol.* 46, 12, 1962.
17. Barlow, J.S. *Electroenceph. Clin. Neurophysiol.* 9, 340, 1957.
18. Bishop, G.H. and J. O'Leary. *Amer. J. Physiol.* 117, 292, 1936.
19. Brazier, M. *Ann. New York Acad. Sci.* 112, 33, 1964.
20. Chang, H.T. *The Evoked Potential. Handbook of Physiology*, 1, Neurophysiology, 1959, p. 12.
21. Ciganek, L. *Rev. Neurol.* 99, 196, 1958.

22. Ciganek, L. Rev. Neurol. 99, 198, 1958.
23. Ciganek, L. Electroenceph. Clin. Neurophysiol. 11, 65, 1959.
24. Ciganek, L. Electroenceph. Clin. Neurophysiol. 13, 165, 1961.
25. Ciganek, L. Ann. New York Acad. Sci. 112, 241, 1964.
26. Cobb, W.A. Electroenceph. Clin. Neurophysiol. 2, 104, 1950.
27. Cobb, W.A. and G.D. Dawson. J. Physiol. (London) 152, 108, 1960.
28. Cohn, R. Electroenceph. Clin. Neurophysiol. 15, 156, 1963.
29. Dawson, G.D. Neurol. Neurosurg. Psychiat. 10, 134, 1947.
30. Dawson, G.D. Electroenceph. Clin. Neurophysiol. 6, 65, 1954.
31. Dumont, S. and P. Dell. Electroenceph. Clin. Neurophysiol. 12, 769, 1960.
32. Gastaut, H. Rev. Neurol. 108, 316, 1963.
33. Ravault, M.P., P. Gerin, C. David, and F. Munier. Arch. d'Ophthalmol. 26, 7, 641, 1966.
34. Voghan, H.G., J.B. Katzman and J. Taylor. Electroenceph. Clin. Neurophysiol. 15, 737, 1963.
35. Voghan, H.G. Ann. New York Acad. Sci. 112, 305, 1964.

S. V. Kravkov Laboratory of Physiological Optics,
Helmholtz Moscow Scientific Research Institute of Eye Diseases

PHOTOREACTIVITY OF THE PIGMENTED EPITHELIUM OF THE EYE

M. A. Ostrovskiy

Detection (by the EPR method) of the appearance of free radicals in the pigmented epithelium and in a suspension of its melanoprotein granules when acted upon by visible light of physiological intensities. When the light is switched off, the free radicals recombine and disappear, thus distinctly manifesting a reversibility effect — namely, the appearance and disappearance of radicals during repeated switching on and off of the light. During illumination by visible light photoconductivity is detected in the pigmented epithelium and the melanoprotein granules by a contactless method at a microwave frequency which makes it possible to study the bulk photoconductor properties of a homogeneous system under heterogeneous conditions. When the light is switched off, the conductivity effect disappears. The photoreactivity of the pigmented epithelium thus shown and certain features of the metabolism and structure of its cells and processes suggest that the pigmented epithelium may play a more significant physiological role in the regulation and realization of the photoreceptor act in the retinal cells (rods and cones) than has hitherto been assumed.

In the mechanism of the visual process the pigmented epithelium is traditionally regarded as a black screen or neutral filter, passively absorbing scattered light within the optic cup. In fact, independently of the conditions of adaptation, of 100 quanta of light entering the eye only 5-6 are effectively absorbed by the photoreceptor elements of the retina (the rods and cones) themselves, the rest being absorbed by the pigmented epithelium [3]. It will be asked how the energy of these quanta absorbed by the black melanoprotein granules is utilized in the pigmented epithelial cell.

/110

The photoreactivity of the pigmented epithelium described in this paper apparently indicates that it can play a rather more active physiological role in the mechanism of regulation or realization of the photoreceptor act in the retinal cells than has hitherto been accepted. Evidence of the photoreactivity of the pigmented epithelium and of a suspension of its melanin granules is given by the appearance of free radicals and of a photoconductive effect during the action of visible light.

1. During recent years the essential role of free radicals in photobiological and enzymic processes has been demonstrated. These processes include the primary processes of photosynthesis and oxidation-reduction reactions.

Free radicals are molecules or fragments of molecules with an unpaired electron and, therefore, existing in an electronically excited state and possessing high chemical activity. They readily take part in chemical reactions, and this accounts for their important role in chemical and biochemical reactions. Besides high chemical activity, they also possess specific magnetic properties, as a result of which they can be detected by the method of electron paramagnetic resonance (EPR). This method has become widely used in biology. However, until very recently, the EPR method has not in fact been applied to the study of primary visual processes. Nevertheless, free radicals may take part in photochemical and enzymochemical processes taking place in the photoreceptors and cells of the pigmented epithelium during the action of light, and investigation of the role of free-radical states of molecules in the mechanisms of vision is highly promising.

The writer and a group of American workers attempted to detect free radicals by the EPR method in specimens of pigmented epithelium and in suspensions of melanin granules illuminated with visible light [1, 2, 4].

The results showed that during the action of visible light at physiological intensities on frozen specimens, unstable light-induced free radicals appear in them (Fig. 1a); these belong to melanoprotein granules contained in large numbers in the pigmented epithelial cell.

/111

During the action of light of constant intensity, the number of free radicals appearing increases, but later the kinetic curve forms a plateau, i.e., dynamic equilibrium is established in which the number of free radicals formed is equal to the number disappearing (Fig. 1b). The height of the equilibrium plateau bears a nonlinear relationship to the concentration of melanin granules in the specimen.

When the light is switched off, the light-induced free radicals recombine and disappear. The rate of appearance of radicals in light and of their disappearance in darkness increases with a rise of temperature. In these experiments on frozen specimens, a reversibility effect was clearly seen. This effect, the appearance of free radicals when the light was switched on and their disappearance when it was switched off, was repeated many times over.

Cope and co-workers [4] and the present writer have recently observed this effect at room temperature and under these conditions have established the times of appearance and disappearance of radicals in the pigmented epithelial cell. Experiments have shown that at 25°C the maximum stationary concentration of free radicals occurs a few seconds after switching on the light, and after the light is switched off they disappear in about 1 sec.

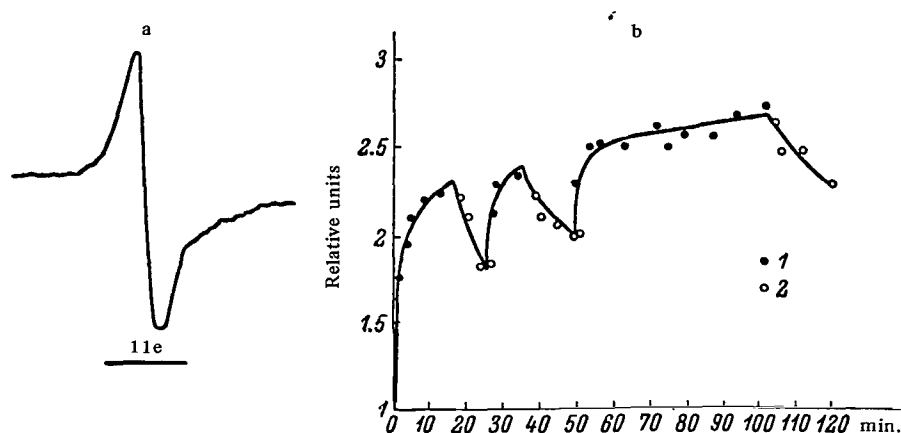


Figure 1. Appearance of Free Radicals in Pigmented Epithelium during the Action of Visible Light at a Temperature of 196°C.

a - EPR-Absorption Spectrum in Illuminated Specimen of Pigmented Epithelium; b - Effect of Appearance and Disappearance of Free Radicals during Switching On and Off of Light. Abscissa, Total Time, in min; Ordinate, Ratio between Amplitude of Light Signal and Dark Signal taken as Unity; 1 - Light, 2 - Darkness.

The photoreactivity of the pigmented epithelium is thus clearly revealed by the series of experiments in which the appearance of free radicals in light and their disappearance in darkness, i.e., the appearance and disappearance of unpaired electrons in the melanoprotein granule, was used as the test.

2. The next step was to investigate the phenomenon of photoconductivity in melanoprotein granules during illumination with visible light, i.e., to study the appearance of a light-induced flux of free electrons in these structures. Theoretical arguments have been put forward to suggest that melanins can be classed as semiconductors [6]. An apparatus has recently been built at the State Optical Institute which can record photoconductivity in organic semiconductors and in biological objects. The first successful experiments were carried out on chlorophyll and on living green leaves.

/112

In conjunction with L.A. Ionov, the writer has demonstrated the phenomenon of photoconductivity in pigmented epithelial tissue and in a suspension of melanin granules during the action of steady bright visible light at room temperature.

Photoconductivity reaches a maximum after 20-30 sec, and its value depends directly on the intensity of the light. When the light is switched off, the effect of photoconductivity disappears. In these experiments too, the pigmented epithelium also clearly exhibited photoreactivity.

DISCUSSION

1. A quantum of light is absorbed in the pigmented epithelial cell by a black melanoprotein granule (0.2μ in diameter and 1μ in length [10]), surrounded by a membrane. In the early stages of development, it is not yet pigmented and possesses a fibrillar structure, the protein in this nonpigmented granule possessing tyrosinase activity [7]. In the process of embryogenesis tyrosine is oxidized in the fibrils to melanin and undergoes polymerization. It has not yet been explained whether the melanin granules possess this structure in the adult state (it probably does), but there is no doubt that the granule contains a chromoprotein, and light thus acts upon the melanin-protein system. It can be assumed that, because of absorption of quanta of light by melanin, free unpaired electrons are formed in such a system, the appearance and increase of photoconductivity and of an EPR signal can be recorded. As a result, activation of the whole melanoprotein molecule must take place: it is in a free-radical state and possesses increased reactivity.

2. How could this photoactivation of the melanin granule be utilized. It may be assumed that the activated granule triggers off a chain of enzymochemical reactions in the pigmented epithelial cells. The fine structure of the pigmented epithelial cells is, of course, highly complex and its metabolic level is extremely high. Besides characteristic pigmented melanin granules, these cells also contain large numbers of giant, longitudinally arranged mitochondria, specific lamellar myeloid bodies, other cytoplasmic structures, and a well-developed endoplasmic reticulum [10], and also a large assortment of the more important enzyme systems and cations [5]. The pigmented epithelial cell gives off up to 20 processes, each 0.7μ in thickness and 10μ in length. The processes insinuate between the photoreceptors and descend to the level of the outer limiting membrane of the retina. Their membranes are in constant and close anatomical contact with the outer membrane of the receptor cell. The number of these cytoplasmic structures in the processes is particularly great. The retino-motor effect of the pigmented epithelium during dark and light adaptation has been shown to consist not of movement of the processes themselves, but of migration of the pigment granules within the process; displacement of the endoplasmic reticulum has also been observed under these circumstances [10]. The mechanism of this migration is still unknown. The important role of the processes of the pigmented epithelium in the exchange of various substances and ions between them and the retina, in the creation of a steady resting potential of the retina, and in the generation of the c-wave of the ERG, which reflects the level of metabolism and active ion transport, has been established [8, 9].

/113

It is difficult at present to identify the physiological effect of the onset of photoconductivity and formation of free radicals of the melanoprotein granules in the pigmented epithelial cell during the action of visible light. The following hypothesis can be put forward.

1. Photoactivation of the melanoprotein granule may act as a trigger for the mechanism of the retino-motor effect of the pigmented epithelium.

2. Indirect photoactivation of the whole pigmented epithelial cell may lead to changes in the level of metabolism in the cell and in the intensity of transport

of metabolites and ions between the processes of the pigmented epithelium and the outer segments of the photoreceptors.

3. The possibility is not ruled out that the pigmented epithelial cell, when excited by light, by virtue of its intimate contact with the membrane of the photoreceptors may have a direct regulatory effect on the functional state of the receptor elements. For example, in the complex, multicomponent process of light adaptation, the pigmented epithelium which is activated by bright light could have a direct inhibitory effect on the receptors, i.e., could serve the function of modulator of photosensitivity of the retina. However, it is too early at present to postulate the mechanism of this effect.

To verify these hypotheses, direct evidence from physiological and biochemical experiments is necessary.

REFERENCES

1. Ostrovskiy, M.A. and L.P. Kayushin. Dokl. Akad. Nauk SSSR., 151, 986, 1963.
2. Ostrovskiy, M.A. In: Svobodno-radikal'nyye protsessy v biologicheskikh sistemakh (Free-Radical Processes in Biological Systems), Trudy MOIP, Moscow, 16, 275, 1966.
3. Pinegin, N.I. In: Soveshchaniye po voprosom fiziologii analizatorov [tez. dokl.] (Abstracts of Proceedings of a Conference on the Physiology of Analyzers), Leningrad, 1961, p. 54.
4. Cope, W.F., R.J. Sever and B.D. Polis. Arch. Biochem. Biophys., 100, 171, 1963.
5. Eichner, D. Z. Zellforsch. 48, 137, 1958.
6. Pullman, A. and B. Pullman. Biochim. Biophys. Acta 54, 384, 1961.
7. Moyer, F. In: G. Smelser (Editor). The Structure of the Eye, Acad. Press, New York, 1961, p. 469.
8. Noell, W.K. J. Opt. Soc. Amer. 53, 36, 1963.
9. Wald, G., P. Brown and I. Gibbons. J. Opt. Soc. Amer. 53, 20, 1963.
10. Yamada, E. In: G. Smelser (Editor). The Structure of the Eye, Acad. Press, New York, 1961, p. 73.

Institute of Higher Nervous Activity and Neurophysiology,
Academy of Sciences of the USSR

NEW DATA ON THE MECHANISMS OF ACTION OF IONIZING RADIATION ON FUNCTIONAL PROPERTIES OF THE RETINA

G. G. Demirchoglyan

Study of the effect of ionizing radiation on the frog retina by recording ERGs from an isolated retina bathed in a nutrient fluid. During the action of the ionizing radiation the b-wave of the ERG is found to be reduced. X-ray stimulation with an intensity of 5 R/sec and a duration of 1 sec evokes a response which is similar to the ERG of a retina exposed to a light stimulus of 0.05 lux and the same duration.

The effect of ionizing radiation on visual functions in man and animals is a problem whose importance has recently increased in connection with the demands of space flights. /114

The visual system is characterized by high sensitivity to ionizing radiation. Work in this field has recently been summarized by Lipetz [4]. Another characteristic feature of the action of ionizing radiation of the retina is its ability to cause direct stimulation of the photoreceptor elements (radiophosphene). Interesting data have been obtained, for example, by D'Arcy and Porter [2], who described how μ -mesons could be detected in cosmic rays by the dark-adapted human eye. On the other hand, ionizing radiation has a significant effect, even in small doses, on the photosensitivity of the retina and on certain other visual functions.

Recently in the writer's laboratory a comprehensive study has been made on the effects of ionizing radiation on various aspects of retinal activity, particular attention being paid to the mechanisms of its high radiosensitivity [1].

To study the mechanisms of radiation effects on the retina, the writer has recently used a technique in which the isolated retina is bathed in nutrient solution. This section of the work was done in conjunction with P. Dettmar. One discovery, in particular, was the active toxic effect of very low concentrations of hydrogen peroxide — a product of radiolysis of water [3] — on the functional properties of the retina. /115

The use of this method for detection of direct retinal responses to ionizing radiation is of particular interest.

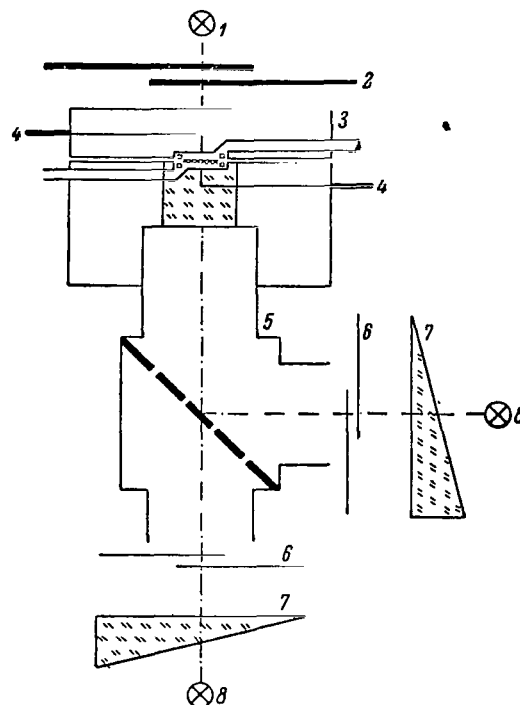


Figure 1. Diagram of Experimental Apparatus.

1 - Source of X-rays; 2 - Lead Shutter;
3 - Chamber made of Organic Material
for Retina (with Inlet and Outlet for
Bathing Solution); 4 - Recording Elec-
trodes; 5 - Transparent Plastic Mount-
ing; 6 - Light Shutter; 7 - Neutral Slab;
8 - Source of Light.

The isolated frog retina was fixed between Perlon rings in a special chamber made of organic material. It was continuously bathed with modified Tyrode solution and illuminated with two sources of light which could be altered with neutral wedges and a light shutter. The ERG was recorded by means of Ag-AgCl electrodes. The source of x-rays (RUM-3 apparatus) was placed above the chamber containing the retina, with a folding lead shutter between them (Fig. 1). The dose rate for the conditions of irradiation used (187 kV, 20 mA), with the lead shutter open, was about 5 R/sec at the position of the retina. The ERG was recorded on a 4-channel electroencephalograph (VNIMIO, type 4 EEG-1) with time constant 0.37 sec.

The graph of one experiment to study the action of x-ray irradiation on the dark-adapted retina in nutrient solution is shown in Fig. 2. It follows from this experiment that during x-ray irradiation the amplitude of the b-wave of the ERG

in response to the test stimulus is reduced. The retina also responds to the beginning and end of x-ray irradiation (circles and crosses standing separately on the figure).

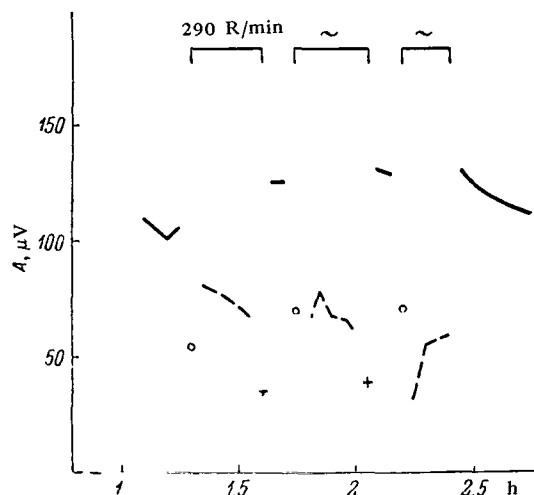


Figure 2. Height of b-Wave of ERG of Dark-Adapted Retina during X-ray Irradiation.

Abscissa, Time in H; Ordinate, Amplitude of b-Wave in μ V. Continuous Line before Irradiation; Broken Line, during X-ray Irradiation. Circles and Crosses Denote Amplitude of Retinal Responses at Beginning (Circles) and End (Crosses) of Irradiation. Intensity of Stimulating Light 0.75 Lux, Duration 1 sec.

Retinal potentials in response to stimulation by x-rays are shown in Fig. 3. They closely resemble the ERG evoked by photic stimulation. The electrical response of the retina to x-ray stimulation with intensity of 5 R/sec and duration of 1 sec (Fig. 3A) is similar to the response of the same retina to a photic stimulus of 0.05 lux \cdot sec and duration of 1 sec (Fig. 3B). During prolonged x-ray irradiation (9 min), a strong d-wave appears in the ERG (Fig. 3C).

The action of light and x-rays on the retina is compared in Fig. 4. Here the height of the b-wave of the ERG evoked by a photic stimulus (against the background of x-ray irradiation) and its response to x-ray irradiation during the action of light are shown.

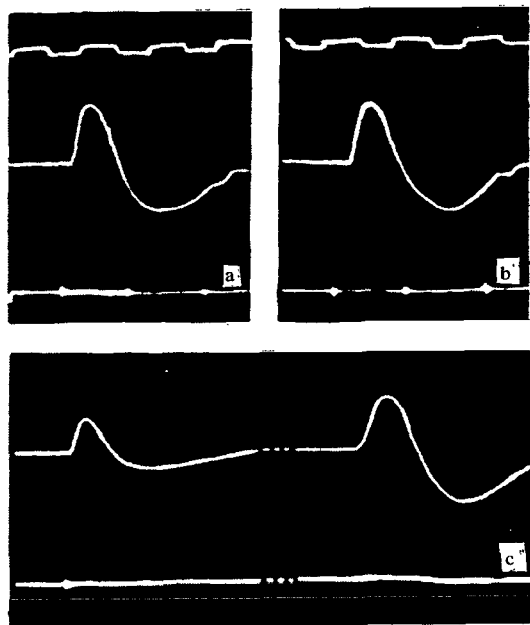


Figure 3. Retinal Potentials in Response to Stimulation.

a - X-ray Irradiation (5 R/sec, Duration 1 sec); b - Photic Stimulation (0.05 lux, Duration 1 sec); Calibration $100 \mu V$, Time Mark 1 sec; c - Switching X-ray Apparatus On and Off Before and After a Period of Prolonged Irradiation (9 min).

When the mechanisms of radiation effects on the retina are assessed, two possibilities must be taken into account: A direct stimulant action of quanta of x-rays on the photoreceptors of the retina and an effect of luminescence of translucent media of the eye (radioluminescence). In the first case, the possible activation of the receptors by a nonphotochemical method is implied, for in the dose ranges used it is unlikely that the rhodopsin will be decomposed, although the possibility of stereoisomeric changes in the rhodopsin molecule by high-energy quanta cannot be ruled out. In the second case, i.e., when secondary mechanisms of excitation are present, the effect of radioluminescence must be detected and assessed quantitatively. Since the essential information required for the assessment is not at present available the question of the mechanisms of radio stimulation of the retina requires further special investigation.

REFERENCES

1. Demirchoglyan, G. G. *Fiziologiya i patologiya setchatki glaza. Pervichnyye mekhanizmy zreniya* (The Physiology and Pathology of the Retina. Primary Mechanisms of Vision), Meditsina Press, Moscow, 1964.

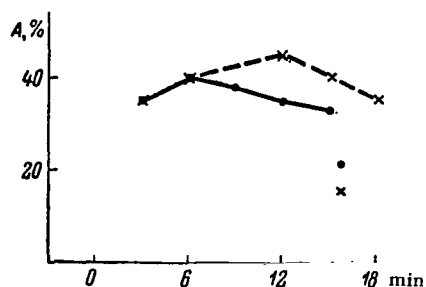


Figure 4. Changes in Amplitude of Retinal Potentials during Photic Stimulation (Continuous Line) and X-ray Irradiation (Broken Line).

Abscissa, Time from Beginning of Stimulation, min; Ordinate, Relative Amplitude of Response, %. Amplitude of Response Before Stimulation taken as 100%. Cross Standing Separately Indicates Potential at Beginning of X-ray Irradiation; Dot Standing Separately Denotes Amplitude of Response at Beginning of Photic Stimulation.

2. D'Arcy, F.I. and N.A. Porter. *Nature* 166, 4858, 1013, 1962.
3. Dettmar, P. and G. Demirtschoglian. *Naturwissenschaften* 51, 269, 1964.
4. Lipetz, L.E. In: *Response of the Nervous System to Ionizing Radiation*. Acad. Press, New York, 1962, p. 45.

Laboratory of Visual Reception,
Academy of Sciences of the Armenian SSR

III. SPACE AND AVIATION PHYSIOLOGY OF VISION

BASIC PROBLEMS OF THE PHYSIOLOGY OF THE VISUAL ANALYZER UNDER EXTREMAL CONDITIONS

Yu. P. Petrov

Survey of the literature on studies of disturbances of visual functions due to action of certain extremal factors. The effects of changes in gravitational conditions, changes in atmospheric pressure and gas composition, mechanical vibrations, and electromagnetic waves of various spectral ranges leading to disturbances such as contractions of the field of vision, reduction of visual acuity, impairment of color vision, hemorrhages, crystalline lens shifts, and pathological vasomotor effects are discussed. Possible mechanisms of these disturbances are suggested.

Man's occupational activity takes place in close interaction with the external environment. Under these circumstances certain environmental factors are extremal and may exert an unfavorable action on visual function, and in some cases they may actually lead to irreversible organic lesions. In the course of development of science and technology new factors acting on the human body and, in particular, on the human visual system have been found, but their effects have so far been studied inadequately or not at all. These factors include:

/118

1. Changes in gravitational conditions — acceleration and weightlessness;
2. Changes in the pressure and gas composition of the atmosphere;
3. Mechanical vibrations and noise;
4. The action of various spectral ranges of electromagnetic waves (ionizing radiation, ultraviolet rays, the visible part of the spectrum, infrared rays and so on).

In the course of phylogenetic development the human body has become adapted to existence under normal gravitational conditions. During flights on modern aircraft and in space flights, man may be exposed to changed gravitational conditions — to acceleration and weightlessness.

Many investigations of the effect of acceleration on the functional state of the visual system have been undertaken in the Soviet Union and elsewhere. These studies have shown that visual disturbances are among the earliest signs of the harmful action of acceleration on the human body. If the rate of increase of acceleration is moderate, the visual disturbances pass through a series of phases. For instance, during the action of acceleration in the head-pelvis direction, initially narrowing of the peripheral field of vision is observed. This is followed by what is known as the "gray veil" accompanied by lowering of the visual acuity and the acuity of color vision, and finally by complete loss of visual functions, the "black veil", which as a rule heralds loss of consciousness. If acceleration increases rapidly in intensity, the sequence of the visual disorders is disturbed or they may be absent and loss of consciousness may take place suddenly, without visual warning.

During acceleration in the opposite direction, the "red veil" appears, and hemorrhages may develop into the sclera, conjunctiva, and retina. Accelerations acting transversely are tolerated best.

Several hypotheses have been put forward to explain the mechanisms of the visual disorders during exposure to acceleration; the most important of these are mechanical, neurogenic, and hemodynamic.

/119

Supporters of the mechanical hypothesis have tried to explain the visual disorders arising during acceleration in terms of mechanical factors (covering of the eyeball with the lid, deformation of the cornea, displacement of the lens, lenticular astigmatism, and so on). If these phenomena do in fact take place during exposure to acceleration, as later research has shown, they are not the main cause of the visual disorders.

The attempt has also been made to explain the visual disorders on the assumption that, during the action of acceleration, as a result of displacement of the viscera, a powerful flow of nervous impulses may be dispatched from the neurogenic zones of these organs and cause the development of protective inhibition in the cerebral cortex, including the visual area. However, this hypothesis completely ignores the hemodynamic changes developing under the influence of modified gravitational conditions, it fails to take into account all the factors, and it has now been rejected.

The basis of the hemodynamic hypothesis is confirmed by the special character of the blood supply to the inner cavity of the eye, namely on the assumption that a blood flow within the eyeball is possible if the pressure in the blood vessels is higher than the intraocular pressures.

When the pressure falls, on account of the hemodynamic outflow of blood during acceleration acting in the head-pelvis direction, the circulation in the eye thus stops and conditions of acute hypoxia develop in the retina. This hypothesis is confirmed by many facts. For instance, in ophthalmoscopic experiments during the action of acceleration, it has been shown [13] that during the appearance of "gray veil" ($g = 4.5$) pulsation of the vessels is observed; this subsequently stops, the vessels of the fundus oculi collapse and come to resemble empty tubes. Some significant experiments with the "ocular plethysmograph" [10] have been carried in this direction. If an additional pressure on the eye is created by means of a special device, visual disturbances occur during lower intensities of acceleration.

During a moderate increase in acceleration, visual disorders evidently develop because of retina ischemia. The disturbance of the phase structure of visual disorders during a rapid increase in the intensity of acceleration is evidently explained by the greater sensitivity of the cortex to hypoxia, on account of which ischemia of the brain and loss of consciousness develop before the onset of visual disorders associated with ischemia of the retina.

Much remains to be explained in connection with these visual disorders during exposure to acceleration and further research into this problem is essential. The effect of acceleration of variable direction and of long-acting acceleration is a problem of great theoretical and practical interest. If disturbances of visual functions are considered from the standpoint of the hemodynamic hypothesis, it can be postulated that the character of the visual field in this case will be different, since hemodynamic changes during exposure to accelerations of variable direction will clearly not be the same as those observed during short exposures to acceleration in a single longitudinal direction. Investigations of prolonged and also of repeated acceleration have shown that the resistance of the body may fall during their action [9]; under these circumstances prolonged transverse accelerations produce a redistribution of blood in the body, and this evidently also leads to a disturbance of the blood supply in different parts of the visual system and changes in its functional state.

/120

The study of effects of weightlessness on the state of visual functions began comparatively recently. Before space flights were started, attempts were made to determine the effect of short periods of weightlessness on visual functions during flights on aircraft-laboratories, and various suggestions were made regarding its possible effect on visual functions. The hypothesis was put forward that, in a state of weightlessness, vision may be disturbed because of lens displacement. Investigations to verify the "lens shift theory" during brief periods of weightlessness, carried out by American workers [16], revealed only a slight decrease in visual acuity ($\sim 6\%$). In the writer's own investigations on an aircraft-laboratory, an increase in the fusion reserves, and a slight vasoconstriction in the fundus oculi were observed during the buildup of acceleration, followed by vasodilatation during short exposures to weightlessness. Accuracy and the time taken to read a specimen text were undisturbed. Other investigations [17] have shown that during weightlessness it is possible to discriminate between objects with lower levels of contrast.

Investigations carried out during short exposures to weightlessness cannot, of course, give a complete idea of changes taking place in visual functions because the weightlessness itself is of such extremely short duration and it is difficult to differentiate its effect from that of the preceding acceleration. For this reason the results obtained must always be interpreted with great care.

Investigations carried out actually during space flights are much more valuable. In fact, the investigations carried out during the first flights yielded unexpected results. This applies to the results obtained by the American astronauts, especially Cooper, Cernan, and others, during the investigation of visual capacity when observing terrestrial objects. These investigations showed that objects distinguished by the astronauts had angular dimensions much less than 1 sec.

Allowing for the action of the atmosphere, which decreases contrast of terrestrial objects, such high values of visual acuity in astronauts are difficult to explain.

Several hypotheses have been put forward to account for these phenomena. Whetmore [18] is skeptical of the truth of Cooper's results and suggests that this astronaut had a disturbance of the visual perception of spatial discrimination resulting from the action of weightlessness and euphoria produced by the interruption of the flow of afferent impulses from muscles and joints. Attempts have been made to explain this high visual acuity by assuming that in a state of weightlessness the intrinsic oscillation of the eyeball may be increased 2-3 times, leading to an increase in the number of perceived objects and, hence, to an increase in the visual acuity. The research methods which we use to determine visual acuity are imperfect and are incapable of revealing the full extent of human functions. In fact, the research methods at present used in occupational selection do not reveal the full extent of a person's functional capacity, and because of this, individual functional reserves are not utilized to their full extent in occupational activity. However, it is impossible at the present to decide which of these authorities is right and to what extent he is right. Only future experiments will resolve this problem. Investigations of other visual functions during space flights have not revealed any significant functional changes. However, remembering that the visual analyzer is one of the principal channels through which information is received, the further study of its functions in a state of weightlessness is of enormous theoretical and practical interest. The fact should be noted that just as during exposure to acceleration, the visual analyzer is more sensitive than any other functional system to hypoxia. Clearly this confirms once again the correctness of the hypothesis that visual disorders during exposure to acceleration are based on retinal and cortical hypoxia resulting from the hemodynamic displacement of blood away from the retina.

/121

The next factor which may influence the visual analyzer is a change in the pressure and gas composition of the atmosphere. The study of the effects of a rarefied atmosphere and a deficiency of oxygen in the inspired air on visual functions began in the early days of aviation, and many papers have been published on this matter. These include some [1, 3, 4] describing investigations of the effect of "altitude" on the state of photosensitivity, accommodation, convergence and [8] study of color vision.

With the development of oxygen equipment capable of supporting human life in a rarefied atmosphere, new factors appeared which could influence visual functions. One such factor is hyperoxia. According to Miller [14] and others, during inhalation of pure oxygen, constriction of the retinal arteries is observed ophthalmoscopically and the visual field is narrowed. In addition, changes in the visual assessment of distance and lowering of the thresholds of color discrimination were found.

The flushing out of carbon dioxide which takes place during inhalation of pure oxygen, resulting in the development of hypocapnia, also is not without its effects on the state of visual function. States of hyperoxia and hypocapnia usually accompany one another, so that their combined effects are observed. This intensifies the picture of changes in the functional state of the visual analyzer.

Mechanisms of change in visual function after change in the partial pressure of gases composing the atmosphere have not yet been fully explained, and so research into this problem, together with the discovery of possible effects of different gas mixtures, will be of considerable practical interest. Work to study the action of chronic exposure to slight degrees of hypoxia and pressure drops will also be of great interest.

The effects of general vertical vibrations on the state of visual functions have been inadequately studied. Among the papers that have been published on this problem of general vibration and its effects on visual functions are those by the German investigator Cörmann [11, 12], who studied these effects of particular frequencies and amplitudes. One function of the visual analyzer which is of great practical importance is the perception and assessment of shapes of objects and their position in space. This capacity is largely determined by visual acuity.

The writer [2] has investigated the direct relationship between the degree of diminution of visual acuity and the amplitude of vibration at different frequencies.

A more complex problem is that of the relationship between the degree of change in visual acuity and frequency. The greatest decrease in visual acuity was observed during exposure to vibrations of 20 and 30 Hz. At frequencies of 60 and 90 Hz, the tendency was again observed for visual acuity to decrease relatively more than at other frequencies.

/122

A study of the effect of prolonged vibrations (for 4 hours) showed that visual acuity is reduced almost immediately after the beginning of vibration. An increase in the duration of exposure produced no further changes in visual acuity, but as soon as the vibrations stopped, visual acuity as a rule was restored to its original level.

Various explanations have been put forward to account for the decrease in visual acuity in man during the action of vibration. Some workers consider that these phenomena are due to changes in the functional state of the visual analyzer; others consider that the visual disorders are based on the transmission of mechanical vibrations to the eyeball, causing disturbance of fixation of the objects of discrimination. The validity of this second hypothesis has been verified experimentally. The fact that the greatest changes in visual acuity occur during exposure to vibrations of 20-30 Hz is evidently explained by the increase in amplitude of vibration of the eyeball as a result of the development of resonance waves in it.

The study of the effect of acoustic stimulation on visual function began many years ago. Examples of such studies are those of Kravkov and Lazarev [6, 7]. However, most investigations have been devoted to the study of the effects of pure tones of average intensity on visual functions, and insufficient attention has been paid to the effects of noise. Individual studies of this factor, undertaken in the period from 1930-1950, showed that noise has a harmful action on the state of visual functions. They showed, for instance, that under the influence of noise the visual field is narrowed, and photosensitivity and discrimination are

reduced. The degree of depression of functions bears a definite relationship to the intensity of the noise stimulus. During the last 30 years, in connection with technological developments, both the spectral composition and intensity of noise have changed considerably; the noise factor has become an important health problem, but although considerable research is going on at the present time to study the effect of noise on the acoustic analyzer, the interaction between the acoustic and visual analyzers and the effects of noise on the state of visual functions are receiving very little attention.

The study of effects of different parts of the spectrum of electromagnetic waves on functions of the human body, including visual functions, is an extremely urgent problem at the present time.

An ever-widening range of the spectrum of electromagnetic waves is being exploited by scientists in the service of mankind. At the same time, virtually all parts of the spectrum which have been studied, with wavelengths ranging from a few millimeters to a few thousandths of an Angstrom unit, are biologically active and may produce not only functional disturbances, but also irreversible organic lesions of the eyes.

For this reason the establishment of permissible norms of exposure is an extremely important problem. Data in the literature on this matter are contradictory and by no means complete. For example, since the time of the discovery of the effect of infrared rays on the organ of vision many years have passed, many powerful sources of such radiation have appeared, yet the data available in the literature deal only with chronic exposure, and no attempt is made to differentiate between their action by convection and by radiation. The permissible norms themselves, for example, in a textbook of diseases of the eye [5] in fact conform to the German standards (DJ No. 4646).

/123

Further investigations must therefore be carried out to study the effects of radiant energy on the visual analyzer. Functional changes and safe, permissible doses must be determined so as to increase the working efficiency of persons exposed to the action of radiant energy, and effective methods of protection must be developed.

In conclusion, it must be pointed out that in most investigations of the effects of extremal conditions, changes in functional thresholds have been studied during exposure to particular factors. However, it is not always possible to judge changes in human working capacity on the basis of threshold changes. For this reason, a future direction of research must be to study the effect of different extremal factors, not only on the functional state of man's visual analyzer, but also on his working efficiency.

REFERENCES

1. Belostotskiy, Ye.M. and S.A. Il'ina. Sov. Zh. Oftal'mol. (Soviet Journal of Ophthalmology) 10, 1, 1937.
2. Borshchevskiy, I.Ya., M.D. Yemel'yanov, A.A. Koreshev, S.S. Markaryan, Yu.P. Petrov, and V.G. Terent'yev. Obshchaya vibratsiya i yeye vliyaniye

- na organizm cheloveka (General Vibration and Its Effect on the Human Body), Medgiz, Moscow, 1963.
3. Vishnevskiy, N.A. In: *Aviatsionnaya meditsina* (Aviation Medicine) Chapt. 7., Medgiz, Moscow, 1941.
 4. Vishnevskiy, N.A. and B.A. Tsirlin. *Fiziol. Zh. SSSR* (Physiological Journal of the USSR) 18, 2, 237, 1935.
 5. Kleybst, B.D. and I.M. Nayman. In: *Rukovodstvo po glaznym boleznyam* (Textbook of Diseases of the Eye) 1, Book II., Medgiz, Moscow, 1962. Chap. 21, p. 239
 6. Kravkov, S.V. *Glaz i yego rabota* (The Eye and Its Work). USSR Acad. Sci. Press., Moscow-Leningrad, 1950.
 7. Lazarev, P.P. and I.Kh. Pavlova. *Dokl. Akad. Nauk SSSR*. 18, 1927.
 8. Mkrticheva, L.I. and V.G. Samsonova. *Dokl. Akad. Nauk SSSR*. 44, 1, 45, 1944.
 9. Savin, B.M. *Vliyaniye peregruzok na funktsional'noye sostoyaniye tsentral'noy nervnoy sistemy i mekhanizmy narusheniya yeye deyatel'nosti* (The Effect of g-forces on the Functional State of the Central Nervous System and Mechanisms of Disturbance of Its Activity), Leningrad, 1966.
 10. Beckman, E.L. *Aerospace Med.* 34, 5, 463, 1963.
 11. Cörmann, R. *Luftfahrtmedizin* (Aviation Medicine) 2, 295, 1938.
 12. Cörmann, R. *Luftfahrtmedizin* (Aviation Medicine) 4, 73, 1940.
 13. Duane, T.D. *Arch. Ophthalmol.* 51, 343, 1954.
 14. Miller, E.F. *J. Aviat. Med.* 29, 598, 1958.
 15. Mozell, W.D. *J. Aviat. Med.* 29, 616, 1958.
 16. Pigg, L.D. and W.N. Kama. Cited in: *Human Factors* 5, 254, 1963.
 17. White, W.J. *Aerospace Med.* 36, 327, 1965.
 18. Whetmore, W.C. *Aviation Week and Space Technology* 78, 24, 34, 1963.

EFFECT OF SPACEFLIGHT FACTORS ON VISUAL FUNCTIONS

Yu. P. Petrov

Study of visual tasks confronting astronauts during space flight, emphasizing the effect of physiological and physical factors acting at various stages of flight on the execution of these tasks. Methods by which the effect of these factors can be attenuated or by which disturbances of the visual functions can be compensated are discussed.

The character of the visual tasks confronting members of the crew of spacecraft is determined by two main factors. First, work with control systems and instruments inside the ship, and second, observations on the surrounding space and the earth's surface.

/124

The most complex problem is that of making observations outside the spacecraft, which includes:

- a) visual orientation and navigation of the ship relative to ground level;
- b) observations of the earth's surface;
- c) observations on celestial bodies and on cosmic space.

The aims and objects of the observations will depend on the purpose of the space expedition.

Successful performance of these tasks will largely depend on the functional state of the astronauts' visual system and also on some factors influencing this state.

Different physiological factors act on the astronaut at different stages of the flight. Spaceflight can be subdivided arbitrarily into three main stages:

- Stage I: launching into orbit;
- Stage II: orbital or interplanetary flight;
- Stage III: return to earth.

In the first and third stages the principal operative factors are acceleration, noise, and vibration.

Visual disturbances are among the earliest signs of the harmful action of acceleration.

As a result of exposure to positive acceleration (head-pelvis) visual disturbances are observed at magnitudes of about 4.0 g, and at 4.7 g complete loss of vision is observed [5], while during exposure to negative acceleration (pelvis-head), at magnitudes of 3 g conjunctival hemorrhages and visual disorders take place [7]. In the case of transverse accelerations in the direction chest-back visual disturbances are observed at much higher magnitudes of acceleration. According to Bührle [3], for example, this magnitude is 14 g, while according to Armstrong [2], it is 12 g. The work of Clarke et al. [4] has shown that if special antigravity suits are worn and specially fitted armchairs used, resistance can be increased to 25 g. The effects of exposure to accelerations in the third stage of the flight will, of course, be greater than in the first stage, because the prolonged weightlessness and adynamia preceding the acceleration reduce the resistance of the human body to accelerations. For this reason, the position of the astronaut in the ship is chosen so that, when the ship goes into orbit, or during the return into the dense layers of the atmosphere, transverse accelerations act on the astronaut.

/125

Investigations [2, 10, 12] have shown that the depression of visual functions during exposure to acceleration, noise, and vibration can be compensated to some extent by an increase in the brightness and contrast of the objects observed. Special attention must therefore be paid to the correct choice of magnitudes of brightness used for the instrument scales and signals in the first and, in particular, in the third stages of flight.

The second stage of flight takes place under the conditions of weightlessness and periodic changes in the photic conditions of the flight.

From investigations carried out by Soviet and American astronauts during spaceflights it can be postulated that weightlessness has very little effect on visual functions. On the contrary, analysis of the results of observations on terrestrial objects made by the astronauts Cooper, Cernan, and others shows that their visual acuity was considerably in excess of 1.0. Remembering that the contrast of terrestrial objects against the background as a rule does not exceed 30%, and also that the layer of the atmosphere reduces contrast of terrestrial objects still more, it is extremely difficult to explain these findings.

Several suggestions have been made to account for these facts. American investigators, for instance, consider that in a state of weightlessness the number of intrinsic oscillations of the eyeball may be increased by 2-3 times compared with that under normal conditions of gravitation, resulting in an increase in the number of patterns perceived by the eye, and an increase in the capacity for fine discrimination. However, this suggestion has not been confirmed and it is unlikely to be accepted.

High values of visual acuity in the case of the American astronauts are most likely to have been due, not to any special causes associated with the space-flight, but to the fact that visual acuity of this type can be found in man under ordinary conditions, except that methods at present used in practice for testing

cannot reveal the full physiological potential of the eye. However, the truth of Cooper's results has been disputed. Whetmore [11] considers that Cooper's statements that he could distinguish small objects in Tibet were the result of visual illusions. In my opinion, such a high resolving power of vision in these astronauts can be attributed to several factors. First, I share to some extent the view of N. V. Shubina that the initial (i.e., under ordinary terrestrial conditions) values of the visual acuity were perhaps higher than 1.0. Second, it may be assumed that the discrimination of objects was based on secondary characteristics, i.e., that objects were deduced. For example, the astronaut could clearly distinguish objects of considerable length, such as a road crossing a river, and imagining that in such a case there must be a bridge, the astronaut "saw" it. When later he saw the wash of a ship, shaped like an acute angle, he "saw" the ship, and so on.

Despite several suggestions, the problem of visual acuity under conditions of weightlessness still remains unsolved and requires experimental investigation.

Results at present available thus indicate that a spaceflight factor such as weightlessness has no significant effect on visual functions. However, it must not be forgotten that the duration of the state of weightlessness in space flights so far undertaken was relatively short. Future flights, especially interplanetary, will be much longer in duration, and in view of possible hemodynamic changes as a result of prolonged exposure to weightlessness, it can be postulated that the state of the visual functions will also be definitely modified. Unusual photic conditions in outer space are a powerful operative factor and can give rise to functional changes in the visual system and, in some cases, they may be harmful. With an increase in altitude above sea level, the ratio between the intensities of direct and scattered solar illumination varies. For example, whereas at sea level the maximal intensity of direct solar illumination is 1×10^5 lux, and the brightness of the sky is 1.6×10^3 nit, above the upper limit of the atmosphere the intensity of direct solar illumination is $1.35-1.4 \times 10^5$ lux and the brightness of the sky 1×10^{-5} nit. The brightness of the solar disk is 2×10^9 nit. As a result, the conditions give rise to very considerable drops of brightness and to the development of very high degrees of contrast. If some object (for example, a space ship) with a coefficient of reflection $\rho = 0.9$ is present in cosmic space, the contrast of the object, illuminated by direct solar rays, with the background (for example, with the cosmic "sky"), will be 4×10^9 . Allowing for the fact that the brightness of the adaptation background may be extremely low, such conditions of illumination will produce a state of blindness and will reduce the visual efficiency of the astronauts. The luminance of objects in outer space will be determined not only by direct sunlight, but also by light reflected by the earth and its cloud cover. According to various workers, the earth's albedo varies from 32 to 42 % depending on the time of year. The albedo of the clouds is 50-55% [1].

Energy values of the solar radiation in cosmic space must next be discussed. The total dose of solar radiation reaching the earth's surface (the solar constant) is $1.4 \text{ cal/cm}^2 \cdot \text{min}^{-1}$, and above the upper limit of the atmosphere it is $2.0 \text{ cal/cm}^2 \cdot \text{min}^{-1}$. This total dose consists of $0.16 \text{ cal/cm}^2 \cdot \text{min}^{-1}$ of ultraviolet radiation, 0.8 of visible, and $1.0 \text{ cal/cm}^2 \cdot \text{min}^{-1}$ of infrared radiation [8].

/126

How does the sun's radiation influence the astronaut's vision ?

The most serious effect of light radiation in cosmic space is the possibility of a chorioretinal burn. Cases of chorioretinal burns by the sun's rays have also occurred under terrestrial conditions during observations of solar eclipses ("solar retinitis"). Above the upper limit of the atmosphere, lesions of the eyes (including burns of the retina) will be 10-50 times more frequent than on earth. Only a few seconds will be sufficient for a burn to be produced [9]. The effect of brief, powerful infrared irradiation has been inadequately studied, but infrared irradiation, combined with visible radiation, will play a definite role in the pathogenesis of chorioretinal burns.

So far as ultraviolet radiation is concerned, not only is the quantity of ultraviolet radiation increased in cosmic space, but its spectral composition also is modified.

At altitudes higher than 40 km, ultraviolet rays in the 220-290 m μ waveband will freely penetrate into the upper layers of the atmosphere and exert some effect on the astronaut's vision.

Radiations between 280 and 292 m μ are the most dangerous to the human eye. The cornea completely absorbs rays shorter than 290 m μ , with the possible development of keratoconjunctivitis and severe hyperemia, a burning sensation, pain, photophobia, and blepharospasm. The possibility that cataracts may develop has not been precisely established, but opacities have been obtained experimentally during exposures to very high doses of ultraviolet rays. The dose of ultraviolet radiation in the waveband from 200 to 400 m μ outside the atmosphere has been shown to be 0.16 cal/cm² · min⁻¹. The threshold dose causing a lesion of the cornea, according to American data, is about 0.15 cal/cm² · min⁻¹. Ultraviolet radiation outside the atmosphere can thus produce visual disturbances. /127

In spaceflight the astronaut will encounter new and unusual factors affecting his visual system. A study of the effect of these factors and the development of methods of protection of the astronaut's eyesight are urgent tasks for future research.

REFERENCES

1. Khrgian, A.Kh. Fizika atmosfery (Physics of the Atmosphere) Moscow, 1958.
2. Armstrong, H. G. and Z.W. Heim. J. Aviat. Med. 4, 199, 1938.
3. Bührle, L. Luftfahrtmedizin (Aviation Medicine), I, 307, 1937.
4. Clarke, N. P., W.M. Wolff and J.J. Gokelmann. Amer. Med. Assoc. Bull. 2, 149, 1965.
5. Cochran, L. B., P. B. Gard and M. E. Norsworthy. Report 001059 02.10 U. S. Naval School of Aviation Medicine, Pensacola, Fla., 1954.
6. Miller, E. F. Aviat. Med. 29, 598, 1958.
7. Sieker, H. O. WADC Tech. Rep. 52-87, Wright Air Development Center, Wright-Patterson Air Force Base, Ohio, 1952.

8. Slager, U. T. Space Medicine, New Jersey, 1962.
9. Strughold, H. and C. Ritter. Aerospace Med. 31, 127, 1960.
10. Urmer, A.H. and E.R. Jones. Human Factors 5, 275, 1963.
11. Wetmore, W.C. Aviat. Week Space Technol. 78, 34, 1963.
12. White, W.J. and R.A. Mouty. Human Factors 5, 239, 1963.

INVESTIGATION OF SPATIAL VISION OF A FLIGHT CREW

K. S. Petrov

Estimation of the absolute distance perception of 100 pilots and navigators with emmetropic refraction and flight experience ranging from 5 to 25 years. The threshold values of absolute distance perception of the subjects are found to lie in the range from 10 to 12 m. It is suggested that this range be taken as the norm for spatial vision of a flight crew.

One function of the organ of vision is estimation of spatial relationships consisting of determination of the remoteness of objects and determination of their position relative to each other (absolute and relative remoteness).

/128

Until recently the spatial vision of flying personnel was estimated from thresholds of relative remoteness determined by means of Howard's apparatus. However, it is clear from the literature that correlation was not always possible between the quality of flight duties and the results of investigation of the ability to judge relative distances. Analysis of the conditions of activity of the pilot's visual system while landing an aircraft shows that the pilot assesses only changes in the distance from an observed object and does not make any oculometric comparison between it and other objects. This is one case of the perception of a change in absolute distance.

Ability to estimate absolute distance was investigated by means of an apparatus designed by Professor Baranovskiy. A combination of stimuli acting on the pilot's organ of vision while examining an object moving within the range from 30 to 50 m is simulated in this apparatus. This distance is optimal during observation of the airfield surface on landing.

We examined mainly fighter pilots (89) transport aircraft pilots (5), and navigators (6). The ages of the subjects were: under 25 years — 6, from 26-30 years — 10, from 31-35 years — 48, from 36-40 years — 17, and over 40 years — 19 persons. The flight experience of the subjects was: under 5 years — 5, from 6-10 years — 15, from 11 to 15 years — 42, from 16 to 20 years — 20, from 21 to 25 years — 12, and over 25 years — 6 persons.

No reference to mistakes in the duties of a pilot which could have resulted from difficulties of visual assessment of distance was found in any of the service

and medical records of the pilots. All those examined showed visual acuity of 1.0 in each eye. The refraction was emmetropic in 73 persons, and in the other 27 there were various anomalies of less than 0.5 D, the physiological normal, were found. Examination of two fighter pilots on large and polaroid diploscopes revealed simultaneous vision.

The method of investigating ability to assess changes in absolute distance was as follows: the subject pressed his face against the mask of the instrument and gazed at a luminous object which could be "moved away" or "brought close" by the physician by turning the head of a microtransmission screw. The screw was turned at the rate of one turn in 4-5 sec. The subject was familiarized with the technique before investigation. The result of the test was the mean of three presentations after the subject had reported verbally a change in the spatial position of the object, "further away" and "nearer" being recorded separately. /129

Threshold values of perception of changes in absolute distance recorded by the aviators are given in the table.

Scale divisions	25	50	75	100	125	150	Total no. of subjects
Meters	Under 2.0	2.01-4.0	4.01-6.0	6.01-8.0	8.01-10.0	10.1-12.0	
Moving away	5	39	41	13	2		100
Moving nearer	3	32	40	21	3	1	100

Smaller threshold values for an object "moving away" were recorded by 65 subjects and for an object "coming closer" by 9 subjects. Equal thresholds of absolute distance for "moving away" and "coming closer" allowing for the error of the method were found in 26 subjects.

All subjects were able to distinguish "moving away" up to a distance of 10 m (125 divisions), and "coming closer" up to a distance of 12 m (150 divisions). The threshold values of perception of absolute distance shown by them can be regarded as normal for the evaluation of spatial relationships by pilots.

These results agree well with the conclusion that threshold values of under 10 m should be taken as the norm of spatial vision for aircrews.

Investigation of spatial vision on the basis of the perception of changes in absolute distance is thus essential for the more accurate determination of the ability of flying personnel to estimate spatial relationships visually.

STUDY OF ACHROMATIC AND CHROMATIC VISUAL SENSITIVITY DURING SHORT PERIODS OF WEIGHTLESSNESS

L.A. Kitayev-Smyk

Study of 30 men subjected to short periods of weightlessness (28 to 30 sec) preceded or followed by g forces while flying in an aircraft along a parabolic trajectory showed changes in the color perception of the subjects. In the case of five of the subjects the field of vision and the light sensitivity were also studied. It was found that under conditions of weightlessness there is an increase in sensitivity to yellow and, to lesser extent, to red. At the same time, in a number of cases the sensitivity to blue-violet radiation decreases. The scotopic vision threshold also decreases, while the field of vision remains unchanged.

The work of Lazarev, Lebedinskiy, Kravkov, and their collaborators revealed changes in human visual functions during stimulation of various analyzers, notably during stimulation of the vestibular and proprioceptive systems. Investigations in recent years have shown that vestibular and proprioceptive reception undergoes considerable changes in man and animals when exposed to one of the most important factors of space flight, i.e., weightlessness. The need for investigation of human visual functions under the conditions of weightlessness is thus apparent.

/130

In 1963, using colorimetric tables, the writer investigated color sensitivity in 28 individuals exposed to short periods of weightlessness, and changes were discovered in 20 of them. If the level of saturation of the color was high, with disappearance of the force of gravity, the perceived brightness of the presented colors was subjectively increased, this effect being most marked in the case of yellow and less marked for red and green; the smallest changes in sensitivity were observed with respect to blue. If the level of saturation of the color tones was low, on the other hand, the perceived brightness was subjectively reduced. Similar results were observed either in the presence or in the absence of fixation on the colored object [2].

The experiments of White [8], carried out under conditions of brief weightlessness, demonstrated an increase in achromatic contrast sensitivity, and the higher the intensity of coloring of the presented object, the greater this increase.

The writer has described narrowing of the subjectively perceived visual field in five of 198 subjects examined during the period of their first exposure to weightlessness during flights along a parabolic trajectory [3].

The object of the present investigation was to determine the sensitivity of peripheral achromatic and central chromatic vision by a quantitative method during exposure to short periods of weightlessness.

METHOD

Conditions of weightlessness lasting 28-30 sec were created in an aircraft flying along a parabolic trajectory. The weightlessness was preceded and also followed by an overload of 1.5-1.8 g lasting 15 sec. In control experiments, weightlessness was produced without the preceding overload.

The sensitivity of peripheral vision was determined by means of an ADM adaptometer; threshold sensitivity was measured during horizontal flight, overloading, and weightlessness. The boundaries of the visual field were investigated by a portable Forster's perimeter along the outer and lower vertical meridians for both eyes.

/131

Contrast sensitivity (by brightness) was investigated by means of an ASR spectroanomaloscope for red, yellow, green, and blue. In addition the subjects were asked to match two shades of green, one a spectrally pure constant color, the other a mixture of blue and yellow mixed in different proportions.

In a series of preliminary experiments carried out during parabolic flights, 50 subjects with normal vision were studied with the aid of special color charts. Thirty of these subjects during weightlessness showed changes in color perception analogous to those described by the writer previously [2]. Of the total number of subjects, five persons with the most constant changes in color perception during weightlessness were chosen, and experiments with the anomaloscope, adaptometer, and perimeter (120 experiments in weightlessness) were carried out on them.

EXPERIMENTAL RESULTS

Determination of the sensitivity of peripheral vision gave similar results in all subjects. During weightlessness the threshold of sensitivity of peripheral vision was lowered; during overloading, whether preceding or following weightlessness, sensitivity rose (Fig. 1).

No changes in the boundaries of the visual field were found in four subjects during weightlessness and overloading. In one subject a slight widening of the boundaries was observed during weightlessness: along the outer horizontal meridian from 90° under natural gravitational force to 97° - 100°, and along the lower vertical meridian from 55° - 58° to 60° - 64°; experiments with the spectroanomaloscope showed that contrast sensitivity to red and, in particular, to yellow increased during weightlessness and decreased during overloading in

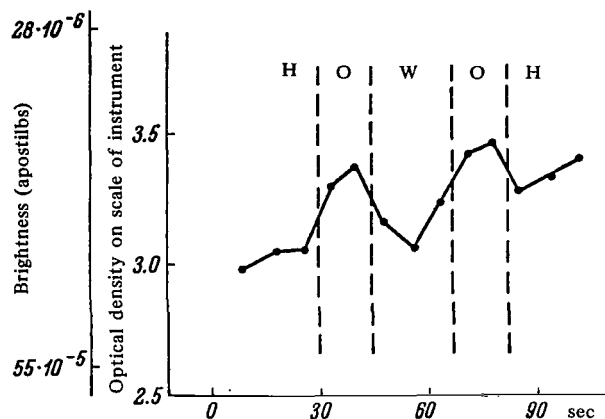


Figure 1. Contrast Sensitivity During Horizontal Flight (h) Overloading (o), and weightlessness (w).

Subject Zh-v. Mean Data for 18 Parabolic Flights.

all five subjects. Contrast sensitivity to blue, on the other hand, decreased (in four subjects). The changes in contrast sensitivity to green were less uniform: in two subjects it decreased during weightlessness and increased during overloading, in one the changes were opposite and in two subjects no changes whatever were found.

/132

In experiments in which a mixed green color was presented, all subjects reported that it turned yellow in weightlessness and blue in overloading.

DISCUSSION

The data described above, as well as the results of the investigations cited, indicate that weightlessness and overloading are stimuli which are not specific for the visual system: they evoke definite changes in its sensitivity. The character and direction of these changes are largely dependent on the intensity of the color or photic stimulus. If this intensity is high enough, an increase in sensitivity to yellow and, to a lesser degree, to red is found in weightlessness. Changes in the sensitivity to colors of the short-wave part of the spectrum were less marked, and indeed, in some cases it was reduced. With a low level of intensity of color stimuli, a decrease in the subjectively perceived brightness of all color tones used in the experiments was found. The threshold sensitivity of scotopic vision also was reduced in the absence of gravitational force. The boundaries of the visual field in persons adapted to weightlessness were virtually unchanged during parabolic flights.

At present the data described above can be analyzed only by comparing them with published data concerning the physiology and pathology of the visual

system and, above all, on changes in the sensitivity of the human retina during exposure to visually inadequate stimuli. A long series of investigations of this problem began in the 1930s with the work of Kravkov et al. [4]. He found by investigation of contrast sensitivity of vision that "the effect of the same inadequate stimulus varies its sign depending only on the intensity of the direct stimulus acting on the tested eye." With a direct stimulus of adequate intensity, according to Kravkov's findings, the sensitivity of vision is increased, at a certain average intensity there may be no changes, and with a direct stimulus of low intensity the level of sensitivity falls. Kravkov postulated the participation of central mechanisms in the origin of these phenomena. The results of investigations of color sensitivity during weightlessness, using chromatic stimuli of different intensities and charts of known colorimetric values fully agree with Kravkov's findings.

In the present investigation, color tones of high saturation produced by the spectroanomaloscope were used. During weightlessness an increase in the contrast sensitivity to red and yellow and, in some cases, to green tones were found. The considerable increase in sensitivity to yellow can be explained by the special properties of the medium-wave part of the visible spectrum. It possesses maximal visibility. It will be remembered that Kravkov spoke of the "peculiar effect of that excitation which corresponds to yellow in the cerebral cortex" [5]. The specific effect of medium-wave tones on the functional stability of chromatic vision was demonstrated by Ye. B. Rabkin [7].

The slight decrease in sensitivity to the short-wave part of the visible spectrum during weightlessness observed in the present investigation can be compared with Kravkov's conception that parasympathicotropic effects lead to a decrease in the sensitivity of vision to blue and green tones, while sensitivity to red and orange colors is increased. The parasympathicotropism of the state of weightlessness has now been demonstrated by several workers [1].

/133

An essential role in the work of the retinal apparatus during weightlessness is unquestionably played by dilatation of the retinal vessels, which has been demonstrated under the conditions of parabolic flight [6].

Further instrumental investigations will be required before the mechanisms of the changes in color sensitivity during weightlessness can be explained.

REFERENCES

1. Bayevskiy, R.M. and O. G. Gazenko. Kosmicheskiye issledovaniya (Space Research) 2, 2, 1964.
2. Kitayev-Smyk, L.A. In: Aviatsionnaya i kosmicheskaya meditsina (Aviation and Space Medicine), Moscow, 1963, p. 246.
3. Kitayev-Smyk, L.A. Problemy kosmicheskoy biologii (Problems in Space Biology), 3, Moscow, 1964, p. 159.
4. Kravkov, S.V. Vzaimodeystviye organov chuvstv (Interaction Between the Sense Organs), Moscow, 1948.
5. Kravkov, S.V. Tsvetovoye zreniye (Color Vision), Moscow, 1952.

6. Petrov, Yu. P. Tezisy 5-go soveshchaniya po fiziologicheskoy optike (Abstracts of the Fifth Conference on Physiological Optics), 1967, p. 112.
7. Rabkin, Ye. B. Tezisy 5-go soveshchaniya po fiziologicheskoy optike (Abstracts of the Fifth Conference on Physiological Optics), 1967, p. 119.
8. White, W. I. Aerospace Med. 34, 327, 1965.

ROLE OF CONVERGENCE IN DISTANCE PERCEPTION DURING THE LANDING OF AN AIRCRAFT

Yu. V. Kamenshchikov

Study of the role of convergence in distance perception in the range from 30 to 50 m in the case of 100 men with normal binocular vision, emmetropic refraction, and visual acuity. It was found that in 75% of the men tested convergence increases the accuracy of estimating the distance from an object from 20 to 50%, while in 25% of the subjects convergence has no effect on the threshold of absolute distance perception.

I. M. Sechenov and I. P. Pavlov deserve the credit for initiating the study of the role of the eye muscles in distance estimation. Sechenov [6] wrote: "Experienced muscle sense corresponding to the degree of divergence of the optic axes is the estimator of distance."

/134

Recent work [1, 3, 4, 5] also points to the active role of eye movements in the perception of depth. Special importance is attached to convergence during the perception of changes in absolute distance, when it is included in a combination of physiological mechanisms giving information about changing distance [2].

To ensure the single vision of an object lying a fixed or varying distance away, reflex convergence occurs. The receptor zone for this reflex is the retina.

It is usually accepted in everyday practice that convergence is unnecessary for fixing objects at a distance of 6 m, and the optic axes are parallel.

Because the pilot determines the height of his aircraft when landing mainly by changes in the size of visible objects and the degree of convergence of the optic axes, and the smallest possible distance of observation under these circumstances is 30-50 m, it was clearly necessary to study the importance of convergence in the perception of changes in the absolute distance as it applies to these conditions. The investigation was carried out with the aid of an instrument for testing the visual estimation of distance designed by V. V. Baranovskiy. It stimulates a combination of stimuli which occur during actual conditions during the observation of an object moving within the range from 30 to 50 m away and back again.

The method of investigation consisted of determining the thresholds of perception of changes in the absolute distance separately for the object when moving away and when coming nearer. Initially they were determined during simultaneous changes in the size of the object and in convergence, and later when the latter were excluded. This was done by shutting off the lens compensator. Tests were carried out on 100 flying personnel with normal binocular vision, emmetropic refraction, and visual acuity of 1.0 in both eyes. The thresholds of absolute distance recorded in these subjects are given in Table 1.

Clearly when the action of convergence is excluded, the thresholds of absolute distance tend to increase, as the increase in their arithmetic mean confirms. This relationship is observed both when the object moves away from the observer and when it moves toward him.

/136

Statistical analysis of the results given in Table 1 showed (Table 2) that the differences observed among the investigated aviators in their perception of changes in absolute distance, depending on whether the whole combination of stimuli were applied or whether convergence was excluded, are substantial and significant.

Next, in the same group of subjects, the individual value of convergence in the perception of absolute distance was determined during a change of distance within the range 30-50 m. The ratio of the thresholds of absolute distance determined with convergence excluded to the thresholds determined in the same subjects when exposed to the action of the combination of stimuli was examined. The results showed that in most subjects the exclusion of convergence from the act of perception of absolute distance leads to an increase in the thresholds. This may possibly indicate an active role of convergence in the assessment of depth when the visual analysis of space is carried out under these conditions.

Convergence gives additional information for 88% of subjects when the object moves away and for 74% of subjects when it moves toward the observer. However, because fluctuations in the results in the same subject sometimes approximate to 10%, disregarding cases of an increase in thresholds of less than 10% it can be said that in the case of an object moving away convergence provides no essential information for 25% of subjects. For the remaining 75% of persons, however, convergence is an additional, informative stimulus, increasing the accuracy of observation in the perception of changing distance from 20 to 50%. On the whole, therefore, it reduces the thresholds by 20-30%, but in a small number of cases it reduces them by 40%, and in isolated cases by as much as 50%.

For an object moving toward the observer, for half of the subjects convergence improves the perception of spatial relationships by 20-30%, and in isolated cases by 40%, whereas the remainder of the subjects perceive changes in absolute distance purely by an increase in the size of the observed object.

It may be asked: are movements of convergence of the eyes of importance on their own account in the assessment of absolute distance of an object moving within the range from 30 to 50 m. To obtain an answer to this question, a further

TABLE 1. Distribution of Thresholds of Perception of Changes in Absolute Distance Depending on Conditions of Observation and Direction of Movement of Object (in % of Number of Subjects Tested)

Direction of movement of object and conditions of observation	Thresholds of absolute distance, m																		Number of subjects tested
	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	
Movement away, change in: size of object and convergence size of object	6	18 8	30 22	19 17	15 22	7 15	3 9	1 3	1 1	1 1	1 1	1 1							100 100
Movement toward, change in: size of object and convergence size of object		1	6 1	14 4	19 18	14 14	17 14	5 11	4 8	3 7	5 5	5 4	3 4	2 5	1 1	1 2	1 1	1 1	100 100

TABLE 2. Statistical Indices of Results Given in Table 1.

Direction of movement of object and conditions of observation	Arithmetic mean \pm mean error of arithmetic mean ($M \pm m$)	Standard deviation ($\pm \sigma$)	Number of observations (n)	Quantitative estimation of significance of differences ($M - M$) with $p = 99\%$		Qualitative estimation of significance of differences $M_1 - M_2$
				obtained	from tables	
Movement away, change in: size of object and convergence size of object	5.13 \pm 0.16 6.26 \pm 0.19	\pm 1.59 \pm 1.94	100 100	}	4.5	2.63
Movement toward: size of object and convergence size of object	8.47 \pm 0.13 9.78 \pm 0.33	\pm 3.07 \pm 3.31	100 100			
						Significant
						Significant

series of experiments was carried out in which the subjects were instructed to determine the direction of movement of an object entirely on the basis of changes in the flow of proprioceptive impulses evoking convergence. By means of the lens compensator of the instrument mentioned previously, the conditions producing movements of convergence and divergence of the eyes accompanying changes in the position of an object in depth were simulated. The object remained constant in size. As was to be expected, none of the subjects was able to evaluate correctly the changes taking place in the spatial relationships, evidently because of the much smaller relative importance of convergence than of changes in the size of the object in the perception of changes in absolute distance under these particular conditions.

It can be concluded that during the observation of movement of an object within the range 30-50 m convergence is of no significant importance as an independent source of information, but it gives additional information to the pilot to enable him to analyze visual space when landing an aircraft, thus improving the perception of changes in absolute distance.

REFERENCES

/137

1. Baranovskiy, V.V. Probl. fiziol. optiki (Problems of Physiological Optics) 12, 239, 1958.
2. Baranovskiy, V.V. Materialy II Vsesoyuznoy konferentsii oftal'mologov (Proceedings of the 2nd All-Union Conference of Ophthalmologists). Tbilisi, 1961, p. 400.
3. Glezer, V.D. Biofizika (Biophysics) 1, 329, 1959.
4. Gurevich, B.Kh. Glazodvigatel'nyye refleksy fiksatsii kak osnova prostranstvennogo zreniya ikak modeli napravlennogo povedeniya (Oculomotor Fixation Reflexes as the Basis of Stereoscopic Vision and as a Model of Directed Behavior), Moscow, 1962.
5. Leushina, L.N. Probl. fiziol. optiki (Problems of Physiological Optics) 12, 314, 1958.
6. Sechenov, I.M. Elementy mysli (Elements of Thought). USSR Acad. Sci., 1943, p. 144.

STUDY OF DYNAMIC VISUAL ACUITY

M. G. Kozyr'kova

Study of the visual acuity of 130 subjects ranging from 20 to 40 years of age, who were required to track an object moving in a horizontal plane. It was found that for an object moving at the rate of 20 deg/sec with an observation time of 1 sec visual acuity is the same as in the stationary test. When the motion of the object is accelerated to 40 deg/sec or the observation time is shortened to 0.5 sec, visual acuity is reduced by 0.1. Each subsequent 20 deg/sec increase in the rate of motion decreases visual acuity by 0.1 to 0.2. In addition, a quantitative study was made of the effect of the direction and duration of the test motion on visual acuity.

A sharp increase in the speed of surface and, in particular, of air transportation is currently taking place. This confronts persons working in certain occupations with the need to distinguish, within a short period of time, objects moving at high angular velocities. However, human visual ability is still largely judged on the basis of visual acuity determined with the aid of stationary signs with virtually unlimited periods of exposure.

/138

The discrimination of moving objects is a more complex problem than the discrimination of stationary objects. It is possible only if the image on the retina remains relatively stationary long enough for it to be perceived. A stationary image is obtained by means of tracking movements of the eyes. The resolving power of the eye, determined during the tracking of moving objects, is called dynamic visual acuity.

The literature concerning the study of dynamic visual acuity is not large. Those investigations of dynamic visual acuity which have been made have shown that with an increase in velocity of movement of an object dynamic visual acuity decreases [1, 4, 5, 6]. The same thresholds of discrimination have been obtained by different workers for different speeds of motion. According to [6], for example, an object subtending $2'43''$ could be distinguished when moving at 10 deg/sec and at 50 deg/sec, while according to [4], it could be distinguished at a speed of 120 deg/sec by persons with identical visual acuity and of the same age. These results are evidently explained by differences between the methods used.

To investigate dynamic visual acuity an instrument permitting motion of an object at speeds of between 20 and 200 deg/sec and exposures of 0.1 sec or more was used. The instrument consists of a projector, a mirror rotated by a motor around a vertical axis, and an examination screen forming an arc of 150° with radius 1 m. The objects are Landolt's rings made from negative film. The rings are projected on to the screen. A shutter is placed between the mirror and screen, and if its gaps are closed the time of exposure of the object on the screen can be changed. The size of the rings is such that visual acuities of 0.05 and from 0.1 to 1.0 with gradations of 0.1 can be determined.

Dynamic visual acuity was determined in 130 subjects aged between 20 and 40 years, with a visual acuity of 1.0. The objects were moved from left to right at speeds of 20, 40, 60, 80, 120, and 160 deg/sec and the exposures were 0.1, 0.25, 0.5, 1.0, and 1.5 sec; observation was binocular. The subject's head was fixed on a chin rest.

The tests showed that for speeds of the object of 20 deg/sec and exposures of 1.5 and 1.0 sec, the dynamic visual acuity was equal to the static. An increase in the threshold of discrimination for exposures of 1.5 and 1.0 sec began with an increase in the speed of motion of the object to 40 deg/sec, when the dynamic visual acuity was 0.1 less than the static.

Each subsequent increase in the speed of the object by 20 deg/sec lowered visual acuity by 0.1-0.2. A decrease in the dynamic visual acuity was observed not only when the speed of the object was increased, but also when the time of observation was shortened. Shortening the exposure time of the object from 1.5 to 1.0 sec had no effect on the discrimination threshold, but shortening from 1.0 to 0.5 sec led to a decrease of 0.1 in the dynamic visual acuity at speeds of 20, 40, 60, 80, and 120 deg/sec. With a shortening of the observation time to 0.25 sec, the faster the object moved the more the dynamic visual acuity was reduced. Whereas for an object moving at 20 deg/sec, shortening of the exposure from 0.5 sec to 0.25 sec lowered the dynamic visual acuity by 1.1 times (from 0.9 to 0.8), at a speed of 80 deg/sec it was lowered by 2.5 times (from 0.5 to 0.2), and at 120 deg/sec by 6 times (from 0.3 to 0.05).

/139

Shortening of the observation time of the object to 0.1 sec still further reduced the ability to distinguish moving objects. The dynamic visual acuity for this exposure, even for an object moving at 20 deg/sec, was 0.4, while at speeds of 80 deg/sec or higher it fell below 0.05 (Fig. 1).

The evident reason for this considerable decrease is that, with this exposure, the moving object is for practical purposes being distinguished by a fixed glance, for the primary reaction time for eye movements is known to be 0.1-0.2 sec [2, 3].

The effect of direction of motion on dynamic visual acuity was investigated for an object moving at speeds 20, 80, 140, and 200 deg/sec and for exposures of 0.5 and 0.25 sec, in 17 subjects using binocular and monocular vision.

The tests showed that when the object moved from left to right the visual acuity for an exposure of 0.25 sec and at speeds of 80 and 140 deg/sec was 0.1

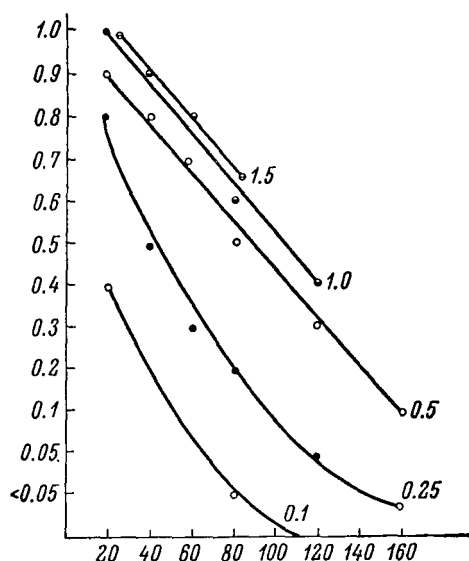


Figure 1. Graph Showing Dynamic Visual Acuity (Ordinate) as a Function of Speed of Motion of Object (deg/sec, Abscissa) and Observation Time (sec). Numbers by Curves Indicate Exposure in sec.

higher than for motion in the opposite direction. At speeds of 20 and 200 deg/sec no difference in dynamic visual acuity in relation to the direction of motion was observed. Evidently if motion is slow and the exposure adequate, the eye can track equally well an object moving from left to right or in the opposite direction.

Tracking movements of the eyes from left to right were assessed by the observers as more satisfactory than movements in the opposite direction. This is perhaps because during reading there is definite conditioning of the eyes to movements successive from left to right.

The binocular dynamic visual acuity for an object moving at a speed of 80 deg/sec and for exposures of 0.5 and 0.25 sec, like the static, was on the average 0.1 higher than the monocular acuity.

/140

Subjects whose static visual acuity was the same could have different values of their dynamic visual acuity (Fig. 2).

The ability of the first subject (Fig. 2) to distinguish the moving object for all exposures specified and at all speeds of motion was much greater than that of the second and third subjects, although all had an identical static visual acuity of 1.0. Persons with a lowered visual acuity, like the fourth subject, also had lower values of dynamic visual acuity under all these conditions. It can accordingly be concluded that perception of moving objects is determined not

only by the static visual acuity, but also by the state of the oculomotor apparatus, by ability to track a moving object, and by other factors.

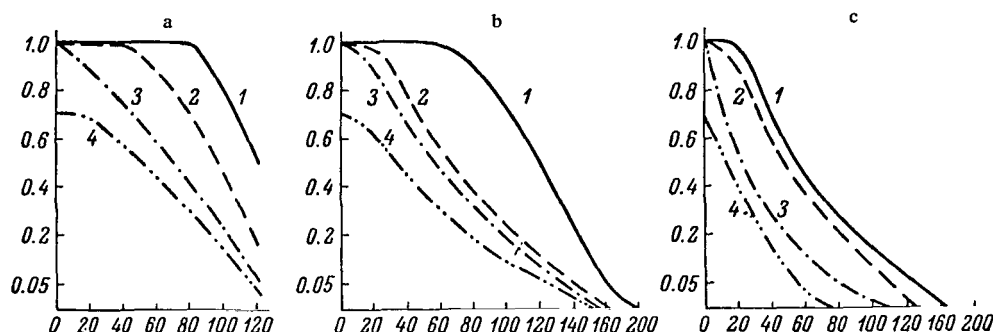


Figure 2. Graph of Individual Differences in Dynamic Visual Acuity of 4 Subjects for Exposures of 1 (a), 0.5 (b), and 0.25 sec (c). Legend as in Fig. 1.

The increase in the threshold of discrimination with an increase in the speed of the object can evidently be attributed to the fact that the tracking system of the eye does not achieve the necessary fixation of the moving object in the region of the fovea centralis of the retina. During tracking the eye repeats the motion of the object at a somewhat slower speed and after a delay of 0.1–0.2 sec (the primary reaction time of eye movement). As a result of this, the image of the object is displaced from the region of the fovea. Displacement of the image on the retina causes blurring and loss of contrast. Since visual acuity depends on contrast, its lowering leads to an increase in the threshold of discrimination. During movement of the image over the retina not only is contrast lost, but the outlines of the object also are distorted on account of superposition of some "blurred" details over others.

To restore fixation, the eye performs corrective saccades, as a result of which it moves for a very short time at a speed equal, or almost equal, to that of the object [2]. With an increase in the angular velocity there is a greater shift of the image on the retina, as a result of which the amplitude and velocity of the corrective saccades increase. If the exposure of the moving object is long enough, there may be several of these corrective saccades, thus improving perception.

CONCLUSIONS

/141

1. Dynamic visual acuity is a complex type of activity of the visual analyzer associated with the perception of moving objects. It is determined by static visual acuity and by the state of the oculomotor apparatus. Its magnitude depends on the speed of motion and the tracking time of the object.

2. Individual differences in dynamic visual acuity observed in persons with the same static visual acuity suggest that there is a good case for using this test for the selection of persons whose activity is concerned with the perception of moving objects.

REFERENCES

1. Shakhnovich, A.I. and V.R. Shakhnovich. Pupillografiya (Pupillography) Moscow, 1964, p. 163.
2. Yarbus, A.L. Biofizika (Biophysics) 7, 1, 64, 1962.
3. Westheimer, G. Arch. Ophthalmol. 52, 6, Sec. 1, 932, 1954.
4. Elkin, S.H. J. Eng. Psychol. 1, 26, 1962.
5. Ludvigh, E.J. Arch. Ophthalmol. 42, 14, 1949.
6. Ludvigh, E.J. and J.W. Muller. J. Opt. Soc. Amer. 48, 799, 1958.

RESTORATION OF VISUAL ACUITY AFTER A BRIGHT LIGHT FLASH OF SHORT DURATION

V.A. Khitun, P.A. Korzun, V.I. Shostak and Ye.A. Obukhova

Presents results on restoration of visual acuity after exposure to flashes of various duration, shape and brightness.

Of the greatest practical importance for many forms of visual work is the rapid restoration of visual acuity after temporary blinding by light pulses.

/142

For this purpose we studied the dynamics of restoration of visual acuity using an arrangement consisting of IFK-2000 pulse lamps that provide a flash, illuminating a transparent dulled screen (Fig. 1), and an ADM adaptometer.

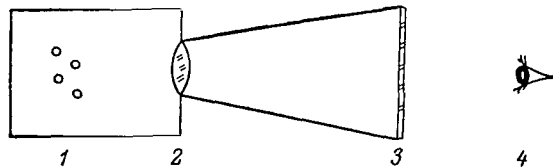


Figure 1. Diagram of the Arrangement for Flash Illumination: 1 - Flash Lamps; 2 - Lens; 3 - Dull-finish Screen; 4 - Eye.

The system provided the following flash parameters: screen illumination - 3,670 candles \cdot sec, screen brightness - 5.52×10^7 nit, and pulse length - 2.1×10^{-3} sec. With this arrangement it is possible to illuminate a retinal area of 8 cm^2 with radiant energy of 0.053 cal, which amounts to 2.3×10^7 lux of illumination on the retina. The visual acuity was determined with an ADM adaptometer at a chart brightness of 0.35 and 0.14 nit.

Two series of tests were run: in the first the time of restoration of visual acuity was determined after flash illumination of the entire retina at two chart brightnesses, and in the second only at one brightness (0.14 nit), but with illumination of the entire retina and of only the central portion (6°). The periphery of the retina was shielded by applying a suitable diaphragm to the flash screen;

during measurements with the adaptometer a tube of black paper was inserted through which the test-chart was observed. Five to six tests were made in each series on each of six observers, 22-27 years of age, with normal vision. The test sequence was as follows: after twenty minutes of dark adaptation, the initial visual acuity was determined on the adaptometer at a chart brightness of 0.14 nit; this was followed by 10 minutes of adaptation to a brightness of 800 nit (ADM "globe") and the dynamics of restoration of visual acuity was established (the time was determined by a timer in accordance with the oral response of the observer). In one session the procedure was repeated for the second test-chart brightness. On another day the restoration of visual acuity was determined in the second test series (with shielding of the periphery of the retina) by an analogous method. The order of presenting the tests and the flash and "globe" alternated.

The results of the statistically processed data we obtained are given in the table and in Fig. 2.

Time of restoration of visual acuity (\bar{t}) with reliability ($\bar{t} \pm 2m$, where $m = \frac{\delta}{\sqrt{n}}$) /143

Visual acuity	Brightness 0.14 nit			Brightness 0.35 nit	
	Mean time of loss of adaptation due to a stimulus			Mean time of loss of adaptation due to a stimulus	
	10 min to a brightness of 800 nit	Flash without shielding	Flash with shielding of the periphery of the eye	10 min to a brightness of 800 nit	Flash without shielding 10 min
0.1	7.67 \pm 1.08	41.8 \pm 7.6	31.6 \pm 6.2	4.69 \pm 0.42	32.2 \pm 5.6
0.2	22.9 \pm 5.2	53.3 \pm 9.0	42.7 \pm 8.4	8.94 \pm 1.86	40.8 \pm 7.4
0.3	36.8 \pm 6.6	65.3 \pm 10.6	54.0 \pm 9.4	13.7 \pm 2.2	48.2 \pm 8.2
0.4	50.3 \pm 9.0	86.8 \pm 14.6	70.8 \pm 11.8	24.5 \pm 8.2	59.3 \pm 9.6
0.5	82.2 \pm 13.8	109.0 \pm 19.4	103.1 \pm 17.6	30.6 \pm 4.6	79.0 \pm 11.8
0.6	127 \pm 22	158 \pm 24	160 \pm 26	46.6 \pm 6.8	95.9 \pm 12.2
0.7	226 \pm 46	225 \pm 28	254 \pm 38	87.5 \pm 14.4	136.7 \pm 18.2

From the data of the table and of Fig. 2 the following conclusions can be drawn.

1. At a brightness of 0.14 nit visual acuity after ten minutes of illumination by a "globe" as well as by a flash with and without shielding of the periphery of the retina returns to the initial state in 4 to 4.5 minutes.

2. Shielding of the periphery does not exert any statistically reliable effect on the dynamics of restoration of visual acuity.

3. At a brightness of 0.35 nit visual acuity returns to the initial state in 2.5 minutes after a flash and in 1.5 minutes after "globe" illumination.

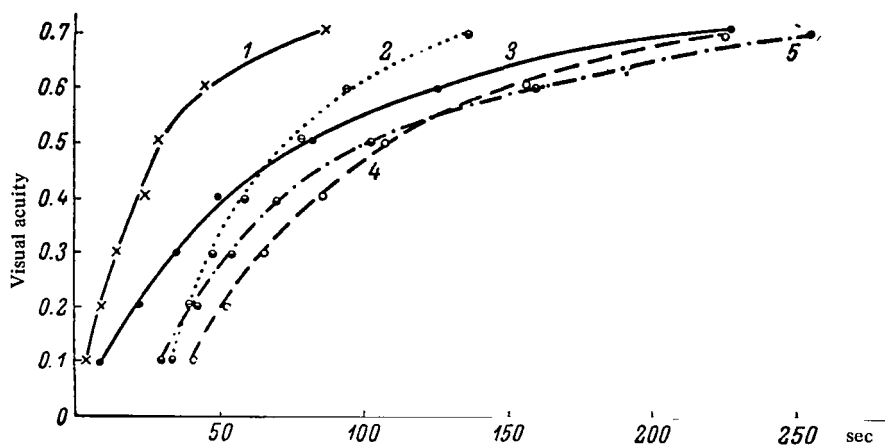


Figure 2. Time of Restoration of Visual Acuity. 1, 2 - Curves for a Brightness of 0.35 nit; 3, 4, 5 - Curves for a Brightness of 0.14 nit.

It should be noted that in some experiments an increase in the final visual acuity after flash illumination was observed, but the data were insufficient for a quantitative evaluation of the observed "exaltation".

CERTAIN FEATURES OF THE EFFECT OF SHORT-TERM SUPER-BRIGHT LIGHT FLASHES AGAINST A BACKGROUND OF TOTAL DARK ADAPTATION

V. I. Shostak

Study of the restoration of light sensitivity in seven subjects exposed to flashes with brightnesses up to 7.2×10^7 to the 7th nits. The electrical sensitivity of the eye, the ERG, the EEG, and the critical frequency of the disappearance of electrical phosphene are also considered. Averaged curves of dark adaptation after ten minutes of light adaptation to a globe brightness of 2500 apostilbs or after diffuse illumination by a flash with a brightness of 7×10^7 to the 7th nits for 2.1 msec are obtained, as well as curves for adaptation after illumination under conditions of shielding the central part of the retina. In the latter case the light sensitivity of the periphery is restored faster, thus attesting to the braking effect of the photopic afferent system on the scotopic system in the presence of superbright stimuli.

Tremendous technical advances have resulted in the appearance of a large number of factors to which man is unaccustomed or which are too intense for him to digest. Among these are super-bright short-term flashes, exposure to which leads to disadaptation of varying degrees of duration. In order to study the mechanisms of this phenomenon, the task was set of investigating the correlation between the psychophysiological data and the objective indicators in man.

In order to generate the super-bright light flashes, a special experimental apparatus was devised which yields flashes of 2.1 msec duration with a maximum brightness of 7.2×10^7 nit, the light pulse on the retina being 0.0066 cal/cm^2 . After such illumination against a background of total dark adaptation, we studied the restoration of light sensitivity with subsequent mathematical processing of the curves of dark adaptation by the method of Academician Lazarev [3], the electrical sensitivity of the eye, the critical frequency of disappearance of flickering electrical phosphene, the bioelectrical activity of the retina, the spontaneous EEG, and the interaction between the photopic and scotopic afferent systems of the optical analyzer.

The restoration of light sensitivity was determined monocularly on the ADM adaptometer by the usual method. Curves of dark adaptation after ten minutes of light adaptation to the surface of the adaptometer globe of brightness 2,500 apostilbs (control) were compared with those after experimental illumination (test). On the basis of 70 studies on seven test subjects, control and experimental adaptation curves were constructed from the average values. Certain qualitative and quantitative differences exist between them.

It is only natural that a stronger decrease in light sensitivity and a subsequent slower restoration to the original state were noted after experimental illumination. Moreover, the experimental curve exhibited a clear inflection point in the segment between 3 and 6 minutes. This fact was first noted by Hecht, Haig and Chase [5] and is interpreted by various authors from different viewpoints. But such a qualitative difference suggests that specific processes governing this feature of restoration of light sensitivity occur in the visual analyzer in response to the action of super-bright flashes.

Light sensitivity is an integral quantity that depends on the functional state of the various links in the visual analyzer. A mathematical analysis of the dark-adaptation curves by the method of [3] permits us to evaluate particularly the participation of the photochemical and central-nervous components.

/145

The suggested formula $E_x = E_0 - E_1 \cdot e^{-a_3 t}$, which describes the dark-adaptation curve, contains quantities reflecting the peripheral and central processes; a_3 is the coefficient of restoration of visual purple and, consequently, gives us an idea of the work of the receptor cells of the retina and characterizes the peripheral sensitivity. The quantity E_0 expresses the maximum light sensitivity and depends essentially on the state of the visual centers.

Having the dark-adaptation curve, it is possible to determine the coefficient a_3 for any instant of time. From the formula proposed by Lazarev it follows that

$$a_3 = \frac{\lg E_1 - \lg (E_0 - E_x)}{tx \cdot \lg e}$$

Also calculated by us were the values of a_3 for all fixed instants of time on the control and experimental curves of dark adaptation, and the average values were found. It turned out that after 10 minutes of disadaptation at a brightness of 2,500 apostilbs, a_3 amounts to 0.142, and to 0.100 after experimental illumination. The difference between them is statistically reliable.

From this it follows that stronger decomposition of the visual pigments occurs after the action of super-bright short-term flashes, but complete decay does not occur. This agrees with certain experimental data which show that the quantity of decomposed rhodopsin does not depend on the brightness if the light flashes are sufficiently short-term.

On the basis of the fact that the quantity E_0 is the same on the control and experimental adaptation curves, it can be concluded that there are no specific differences in the centers of the visual analyzer at this instant of time (i.e., at the 60th minute).

Thus, a mathematical analysis by P.P. Lazarev's method showed that when super-bright short-term light flashes are applied, processes in the peripheral portion of the visual analyzer play an important part in the mechanisms of disadaptation.

The interaction between the photopic and scotopic afferent systems was studied by comparing the dark-adaptation curves after illumination of the entire

retina by an experimental flash and after screening the central portion of the retina (8°). In both cases the light sensitivity was determined while projecting the test object onto 12° of the periphery of the retina.

On the basis of the above-mentioned 70 studies carried out on seven test subjects, dark-adaptation curves obtained under identical circumstances were plotted from the average values. It was found that the restoration of the light sensitivity after illumination while screening the central portion of the retina takes place at a faster rate than without screening. A statistically reliable difference exists over a period of 20 minutes, the greatest difference (0.36-0.42 logarithmic units of light sensitivity) being noted in the interval between 6 and 12 minutes. This indicates that the photopic system of the eye has a retarding effect on the scotopic system when exposed to super-intense stimuli, and this fact probably plays a definite part in the disadaptation mechanisms. Beginning with the studies of Müller [7], a discussion has been carried out on the mechanisms of this interaction. Taking into account the data on subtle functional interrelations between retinal elements [4, 2], it can be said that the reciprocal relationship between the two afferent systems is realized according to a complex mechanism connected with the activity of both the peripheral and central links of the visual analyzer.

/146

The data obtained in this study also enable us to express a definite opinion as to the point of inflection in the interval between 3 and 6 minutes on the dark-adaptation curve after super-bright illumination. As is well known, there are two viewpoints on this question. On the one hand, Kohlrausch [6], Hecht, Haig and Chase [5] have considered that this phenomena is contingent on transition from photopic to scotopic vision. On the other hand, Bogoslovskiy [1], Rushton and Baker [8] have explained this feature as central-nervous processes. The data we obtained in a series of tests aimed at determination of the electrical sensitivity of the eye, recording of the bioelectrical activity of the retina and of the brain permit us to adhere to the old viewpoint.

Thus, the effect of short-term super-bright light flashes is to generate a number of specific features in the visual analyzer that have a definite significance in disadaptation mechanisms.

REFERENCES

1. Bogoslovskiy, A.I. Problemy fiziologicheskoy optiki (Problems of Physiol. Optics) 2, 136, 1944.
2. Byzov, A.L. Elektrofiziologicheskiye issledovaniya sechatki (Electrophysiological Investigations of the Retina), Moscow, 1966.
3. Lazarev, P.P. Issledovaniya po adaptatsii (Research in Adaptation), Izd. AN SSSR 1947.
4. Lebedinskiy, A.V. Trudy 1-oy konferentsii po fiziologicheskoy optike (Proceedings of the First Conf. on Physiol. Optics) 27, 1934.
5. Hecht, S., C. Haig and A.M. Chase. J. Gen. Physiol., 19, 321, 1937.
6. Kohlrausch, A. Pflüg Arch. f. Physiol., 196, 113, 1922.
7. Muller, G.E. Z. f. Sinnesphysiol., 54, 1923.
8. Rushton, W.A.H. and H.D. Baker. Nature, 200, 421, 1963.

IV. OPTICS AND HISTOCHEMISTRY OF THE EYE, RESEARCH METHODS

ON THE PROBLEM OF THE REFRACTION OF THE FISH EYE

P. B. Bogatyrev

Refraction was investigated in 11 species of freshwater fishes from the central zone of the RSFSR and 9 species of exotic aquarium fishes of different ages by the anatomical-optical method with rapid freezing of the eye. Three different types may be distinguished in the optics of the fish eye in relation to the relative position of the crystalline lens and the retina. Type 1 comprises those fishes in whom the center of the crystalline lens coincides with the center of the retinal hemisphere, so that the eye has a relatively narrow zone of sharp vision confined to objects very close to it in space: between 1 and 10 cm in adult fishes and even less in young fishes. The refraction of such eyes is of the myopic type. Carp, crucian carp and carp-bream are of this type. The eyes of fishes of type 2 are capable of adjustment for sharp vision on very near objects and on objects at considerable distances. In them refraction is different along the different optic axes and emmetropic along the central axis. Pike, pike-perch, perch, roach, bleak and other fishes have vision of this kind. The eyes of the eel and the trout are of the third type; here the zones of sharp vision are differently arranged from that in fishes of type 2, but these fishes also possess the capacity for differential focussing for the simultaneous viewing of objects at different optic angles and at different depth.

Most investigators [8-11] who have studied the refraction of the fish eye have discovered myopia in the overwhelming majority of bony fishes. Nevertheless, data obtained by later research [7, 12] have shown that hyperopia or even emmetropia is characteristic of the eyes of most fish species.

/147

In view of this situation regarding the types of refraction of fish eyes, the author carried out a series of investigation under the direction of B. P. Manteyfel'. Studies were made of the eyes of 11 species of freshwater bony fishes from the central zone of the RSFSR and 9 species of exotic aquarium fishes of different ages.

Freshwater fishes from the central zone of the RSFSR	Exotic freshwater aquarium fishes
Carp (<i>Cyprinus carpio</i>)	<u>Brachydanio rerio</u>
Goldfish (<i>Carassius auratus</i>)	<u>Cichlasoma brilliantum</u>
Crucian carp (<i>Carassius carassius</i>)	<u>Pterophyllum scalare</u>
Roach (<i>Rutilus rutilus</i>)	<u>Hetichromis bimaculatus</u>
Carp-bream (<i>Abramis brama</i>)	<u>Macropodus opercularis</u>
Lake trout (<i>Salmo trutta morpha lacustris</i>)	<u>Trichogaster trichopterus</u>
Eel (<i>Anguilla anguilla</i>)	<u>Epiplatys chaperi</u>
Perch (<i>Perca fluviatilis</i>)	<u>Lebistes reticulatus</u>
Pike-perch (<i>Perca lucioperca</i>)	<u>Cichlasoma nigrofasciatum</u>
Pike (<i>Esox lucius</i>)	
Verkhovka (<i>Leucaspis delineatus</i>).	

Bearing in mind that the fish eye differs from the eye of terrestrial vertebrates in that the crystalline lens is round and has a fixed focal distance, and is also the sole dioptric element of the eye [12, 13], we employed the anatomical-optical method in the present study, using the formulas of geometrical optics.

A freezing microtome was used in histological treatment of the eyes of the fishes investigated. The tissues are less distorted when this method is used than when other histological methods are used [6]. In our experiments the eyes removed from the fish head, or the entire head including the eyes in the case of small fishes, were placed on the microtome stand and frozen by liquid carbon dioxide. The layers of optic tissue were sectioned from above downward until the microtome knife reached the center of the crystalline lens. Cross sections were usually cut along the central optic axis through the center of the crystalline lens and the middle of the retina in two mutually perpendicular planes with the eye horizontal and vertical.

After a section had been cut it was photographed by means of a photographic reproducing attachment employing a "Zenit" camera with mirror and spacer rings for macro-photography.

/148

Subsequently we studied only the prints of the photographs taken from cross sections of the fish eyes at known magnification.

The linear expansion of the vitreous body on freezing was on average approximately 8% of the initial length, and this was subsequently taken into consideration when making calculations.

On the basis of the photographs obtained we proposed a provisional division of the eyes of the fish species investigated into three different types according to the relative position of the crystalline lens and the retina. Difference in the structure and relative position of the parts of the optical system of the fish eye has a definite effect on the location of zones of sharp vision for fishes of different ecology. We therefore examined in this study the zones of sharp vision for each type of fish eye separately.

The formulas of geometrical optics were used to calculate the zones of sharpness. When finding the distance from the fish eye to the focal point we made use of the basic lens formula

$$\frac{1}{a} + \frac{1}{b} = \frac{1}{f}, \quad (1)$$

where a is the required distance from the focal point to the anterior nodal point of the crystalline lens of the fish eye; b is the focal distance of the crystalline lens, i.e., the distance from the posterior nodal point crystalline lens to the posterior portion of the retina; f is the focal distance of the lens of the fish eye.

In each specific case the value of b was taken from the photograph and converted for the magnification of the photograph, allowing appropriately for the linear expansion of the vitreous humor on freezing.

The focal length (f) was found from the radius of the crystalline lens by the corrected formula of Matthiesen:

$$f = 2.55 r \left(-\frac{1}{2} r \right), \text{ or } f = 2.05 r, \quad (2)$$

where r is the radius of the crystalline lens; $1/2r$ is the distance from the center of the crystalline lens to the anterior and posterior nodal points.

Having calculated a value for the required quantity (a), i.e., the distance to the focal point for each case, we determined the anterior and posterior limits of sharpness (Γ_{sp} and Γ_{sa}) using the approximate formulas derived by Gal'perin [2] and Lapauri [3], which are respectively

$$\Gamma_{sp} = \frac{af^2}{f^2 - akz}, \quad (3)$$

$$\Gamma_{sa} = \frac{af^2}{f^2 + akz}, \quad (4)$$

where k is the denominator of the aperture ratio, z is the circle of confusion.

The aperture ratio denominator (k) for formulas (3) and (4) may readily be found from the focal length of the crystalline lens (f) and the diameter of the crystalline lens (d) by the formula

$$\frac{1}{k} = \frac{d}{f}, \text{ or } \frac{1}{k} = \frac{2r}{2.05r} \quad (5)$$

Hence for most adult fishes the value of (k) will be close to 1. For some fishes, for example for the eel or for the young of a number of fishes, the value for (k) will be slightly greater than 1.

The size of the circle of confusion (z) for a whole series of fishes 15-20 cm long is 0.001 mm, and since the variation of visual acuity as a fish grows is practically proportional it may be considered with some degree of approximation that the size of the circle of confusion will vary in inverse proportion to the growth of the fish.

When the distance to the anterior and posterior limits of sharpness (Γ_{sa} and Γ_{sp}) is known, it is a simple matter to find the required value of the depth of the sharpness zones (Z_s) by the formula:

/149

$$Z_s = \Gamma_{sp} - \Gamma_{sa} \quad (6)$$

When this formula is written out in full

$$Z_s = \frac{af^r}{f^r - akz} - \frac{af^r}{f^r + akz}, \quad (6a)$$

it is readily appreciable that there is no foundation at all for the assertions of some specialists that fishes are near-sighted merely on the basis that their eyes have a spherical crystalline lens, since the spherical crystalline lenses of fishes always have a shorter focal length than the flattened crystalline lenses of the same diameter of other vertebrates and will consequently have a relatively greater focal depth.

In order to determine the position of the zones of sharp vision of a fish in space we used photographs of horizontal and vertical cross sections of fish eyes through the center of the crystalline lens and the middle of the retina of the same fish. Constructing optic axes at different angles to the central optic axis, as depicted in Fig. 1, we took from the photograph of the horizontal section of the eye the measurements of focal distance along each optic axis constructed, denoting them by b_1, b_2, b_3, b_4 , etc.

Assuming the focal length of the crystalline lens of the fish eye to be constant at all viewing angles, it is a simple matter to find from formula (1) the corresponding positions in space of the focal points and their distances along the optic axes, denoting them by a_1, a_2, a_3, a_4 , etc. By joining these focal points we obtain a line which we call the focal line of the fish eye. In addition, the limits of the zone of sharp vision may readily be found from formulas (3) and (4) in each specific case for each value. Successively joining up first all the points of the near-limits of the zones of sharpness and then all the points of the far-limits we obtain a graphic depiction of the zone of sharp vision within the limits of a monocular field of vision in the horizontal optic plane of the fish under investigation (Fig. 2).

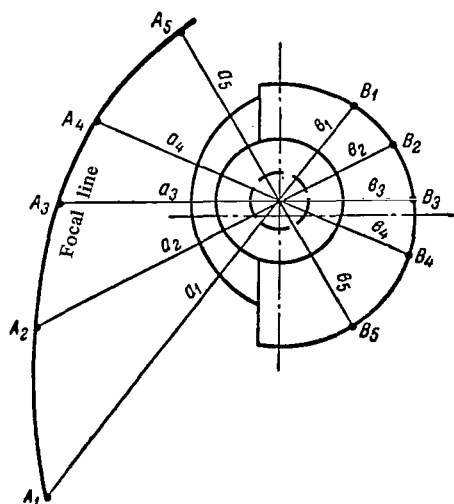


Figure 1. Measurement Data of Disturbances to Focus on Each Optic Axis Constructed.

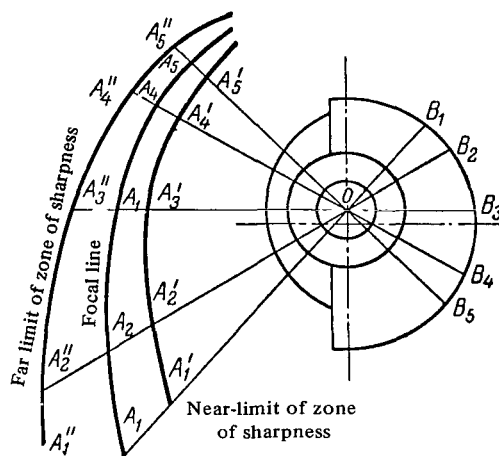


Figure 2. Graphic Depiction of the Zone of Sharpness of Vision Within a Monocular Field of Vision in the Horizontal Plane of an Investigated Fish Eye.

As has already been stated, the location of the 3-dimensional zones of sharp vision, which in this case determines the refraction of the fish eye, will be considered in the horizontal and vertical planes separately for each structural type of the fish eye.

RESEARCH RESULTS

/150

Refraction in the First Type of Fish Eye

On the basis of the structure of the anterior media of the fish eye we have classified as belonging to the first type those eyes in which the center of the crystalline lens coincides with the center of the retinal hemisphere, and since the principal nodal points of the crystalline lens are located on a spherical surface around its center it may be considered that they are all equidistant from the retina. Consequently, all the focal distances, i.e., the values of b for all the axes constructed in the fish eye through the center of the crystalline lens to the retina are equal. It will readily be noted that in this case all the values for distance to the focal point a will also be equal and will lie on a hemispherical surface around the center of the crystalline lens. It may be considered on the same basis that the anterior and posterior limits of the zone of sharp vision will be located as hemispheres also around the center of the crystalline lens.

Figure 3 (a, b) is an approximate depiction of the position of the focal points and the limits of the zone of sharpness in the horizontal plane of the section for fish eyes of type 1 without allowance for accommodation.

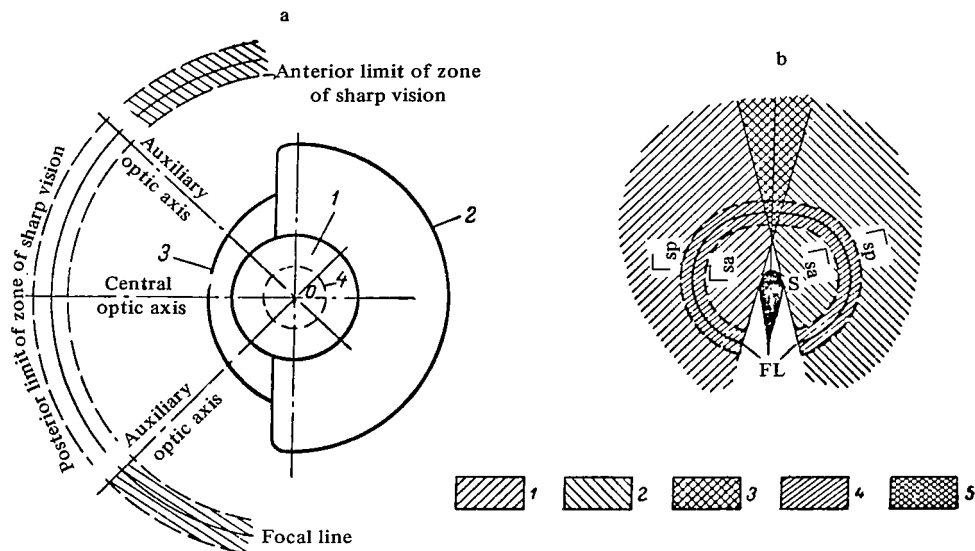


Figure 3. Refraction of the First Type of Fish Eye.

a) Refraction Diagram: 1 - Crystalline Lens; 2 - Retina; 3 - Cornea and Anterior Chamber of the Eye; 4 - Line of Nodal Reference Points; O - Center of Crystalline Lens and Center of Retinal Hemisphere.

b) Locational Diagram of the Zone of Sharp Vision: 1 - Monocular Field of Vision of the Left Eye; 2 - Monocular Field of Vision of the Right Eye; 3 - Binocular Field of Vision of Both Eyes; 4 - Zone of Sharp Vision of the Monocular Fields of Both Eyes; 5 - Zone of Sharp Vision of the Binocular Fields of Both Eyes. S - Section of the Fish Body in the Horizontal Plane; FL - Focal Line of the Right and Left Eyes; Γ_{sa} - Anterior Limit of the Zone of Sharp Vision; Γ_{sp} - Posterior Limit of the Zone of Sharp Vision.

Reasoning in the same way, it may readily be established that the same location of the zone of sharp vision is also to be observed in the vertical plane of the cross section of the fish eye.

Making the appropriate calculations from formulas (2), (3), (4) and (5) we found that fish eyes of the first type in a state of rest are focussed for clear vision only of objects situated very close to them in space and have a comparatively narrow zone of sharp vision. The location of the near-limit which determines the location of the zone of sharpness of the space depicted varies within certain limits in the adult fishes investigated between 1 and 10 cm depending on the species and size of the fish. This distance is far smaller in the young of the fishes investigated. It therefore follows that myopia is the type of refraction of such eyes.

/151

The structure of the anterior media of the eyes of these fishes and the location of the zone of sharp vision are determined by their benthic, relatively immobile mode of life. There are few fish species in which this type of eye has been discovered. They include carp, large goldfish and carp-bream which are in

the main benthophages that obtain their food in deep ooze. Sight is necessary for these fishes mainly for orientation in the water and for spawning interrelationships and is only of secondary importance in the obtaining of food.

Refraction in Fishes of Type 2

We classified as belonging to Type 2 fishes in whom the center of the crystalline lens in horizontal cross sections of the eyes was displaced to the anterior portion of the eye away from its central axis.

Employing geometrical optics for deliberations and calculations similar to those made previously, we found that the focal line in the horizontal plane on which the focal points of the fish eye are located lies at different distances from the center of the crystalline lens.

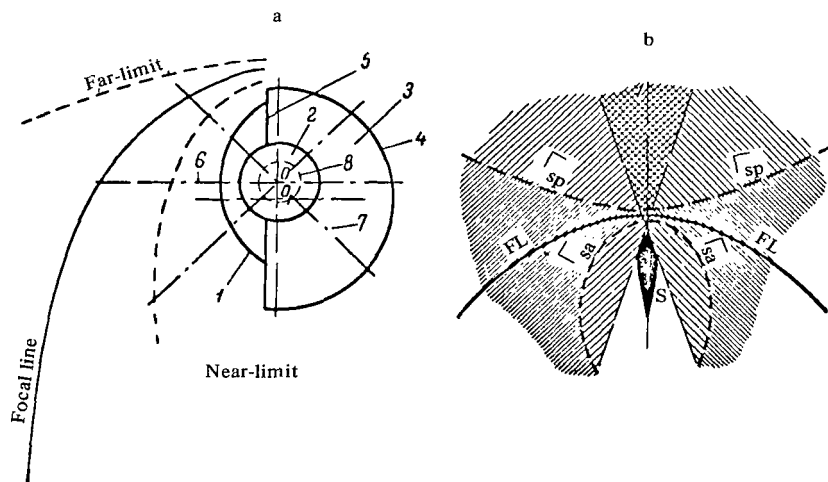


Figure 4. Refraction in Fishes of the Second Type.

a) Diagram of the Refraction of the Fish Eye: 1 - Cornea and Anterior Chamber of the Crystalline Lens; 2 - Crystalline Lens; 3 - Vitreous Humor; 4 - Retina; 5 - Iris; 6 - Central Optic Axis; 7 - Auxiliary Optic Axes; 8 - Line of Nodal Points of the Crystalline Lens; 0 - Center of the Retinal Hemisphere; 0₁ - Center of the Crystalline Lens. b) Locational Diagram of Zones of Sharp Vision. Key as in Fig. 3a, b.

Figure 4, a depicts the structure of the anterior media of the eye in the horizontal plane for fishes of type 2 and a case similar to that considered for the eye of a fish of type 1 showing calculation of the focal points located along the axes at different angles to the central axis for the given type of eye.

In this case, as we have previously described, we took measurement data for the focal distances of the fish eye investigated and then found the corresponding distances from the anterior nodal points to the focal points from the basic lens formula (2). After this we found the near and far-limits of the sharply depicted space from formulas (3) and (4), and then employed formula (5) to determine the depth of the zone of sharpness of the corresponding areas of space seen by the fish. Figure 4, b is a generalized diagram of the limits of the zone of sharp vision both for one eye and for two eyes with allowance for their position on the head of the fish investigated. /152

It should be noted that fishes classified by us as belonging to type 2 in terms of eye structure are the most prevalent among the bony fishes. They include pelagic schooling fishes (bleak, verkhovka), a number of predators (pike, pike-perch, perch) and some mixed feeders (roach); from among the aquarium species they include the guppy.

The eyes of the young of all the fish species investigated by us may be classified in terms of their structure as belonging to type 2, and in a number of instances the displacement of the crystalline lens is more clearly expressed in them than in the adult fishes.

Making similar calculations for vertical cross sections of the fish eyes we established the similar location of the zone of sharp vision in the vertical sectional plane.

It is evident from the diagram (Fig. 4) that the eyes of a fish of type 2 are capable of focussing for sharp vision in a state of rest on objects situated very close to the anterior portion of the head and at the same time they are capable of sharp perception at a considerable distance of objects located in and to the rear of the region of the central optic axis.

The calculations showed that for most of the fishes investigated by us the zone of sharp vision in the region of the central optic axis and also along optic axes situated at angles in front of the central axis is very close to the head of the fish. The location in space of the limits of the zone of sharp vision and of the focal line is dependent on the species and size of the fish and ranges between 0.1 and 5 cm.

Along optic axes lying in the horizontal plane at an angle of more than 30° behind the central optic axis the far-limit of the zone of sharpness in these fishes lies at infinity, and the focal line lies beyond the hypofocal distance. Consequently, the near-limit of the zone of sharp vision lies at a considerable distance from the fish eye, sometimes reaching several tens of centimeters.

It may be concluded from the foregoing that the type of refraction will be different for fishes of type 2 along different optic axes. For most of the species investigated by us emmetropia is observed along the central optic axis. Emmetropia will also be the case observed along all optic axes situated in the vertical plane passing through the central optic axis of the fish.

The type of refraction along optic axes situated in the horizontal plane and lying in front of the central optic axis by an angle of more than 20° will be myopia.

Hyperopia of the eye will be observed along optic axes lying in the same horizontal plane at angles of more than 30° .

This type of refraction of the eyes in fishes of type 2 is in full agreement with their ecology. As has already been noted, this category of fishes comprises planktophages, small forms feeding on plankton, mixed feeders, schooling fishes and most of the predators. The eyes are well developed in all these fish species and they need sight to obtain food and discover enemies, for orientation in space and in the school and also for courtship etc. [1, 4, 5]. This simultaneous differential focussing of the eye in a state of rest enables small fishes, while clearly distinguishing small food in the immediate vicinity of the mouth, at the same time to see an approaching predator from the side, from below, from above and from the rear at a considerable distance; it also enables schooling fishes when feeding on plankton simultaneously to see their partners in the school and note the movement of each of them.

/153

Refraction in a Fish of Type 3

This group of fishes is not very abundant. From among all the fishes investigated by us we included in it only two species, namely the eel and the lake trout.

The basic structural feature of the eye of a fish of type 3 is the location of the retina relative to the crystalline lens, in which the center of the latter is slightly displaced from the center of the retina sphere toward the outside of the eye, along its central axis.

Employing optical formulas and using the same methods as were used in investigation of the refraction of the eyes in fishes of types 1 and 2 we calculated the position of the focal lines and the limits of the zone of sharp vision for horizontal and vertical sections of eyes of this type and found that the location of zones of sharp vision and their horizontal and vertical dimensions did not differ significantly. Figure 5, a is an approximate diagram of the location of the focal line and the zone of sharp vision for the eyes of a fish of type 3 in the horizontal plane: there is also an approximate diagram of the location of the zone of sharpness for the entire fish with allowance for the position of its eyes (Fig. 5, b).

It is evident from the diagram that the eyes of fishes of type 3 have the same differential focussing for the simultaneous viewing of different objects located at different viewing angles and at approximately the same distances as for the eyes of fishes of type 2. Nevertheless, there are significant differences in the refraction of these two types of eyes. As is evident from the diagram in Fig. 5, these differences are that the eyes of a fish of type 3 clearly discern remote objects in the anterior sector of the viewing angle, and the far-limit of the zone of sharp vision lies at infinity. In this case the refraction of the eye assumes the form of hyperopia by comparison with myopia in the corresponding sector of the viewing angle for the eyes of fishes of type 2. Myopia is observed along the central optic axis of a fish of type 3 by comparison with the emmetropia of the

/154

corresponding sector of the eyes of a fish of type 2. The form of refraction in the posterior lateral sector of vision in the eye of a fish of type 3 will correspond to an eye of type 2 and will be hyperopia.

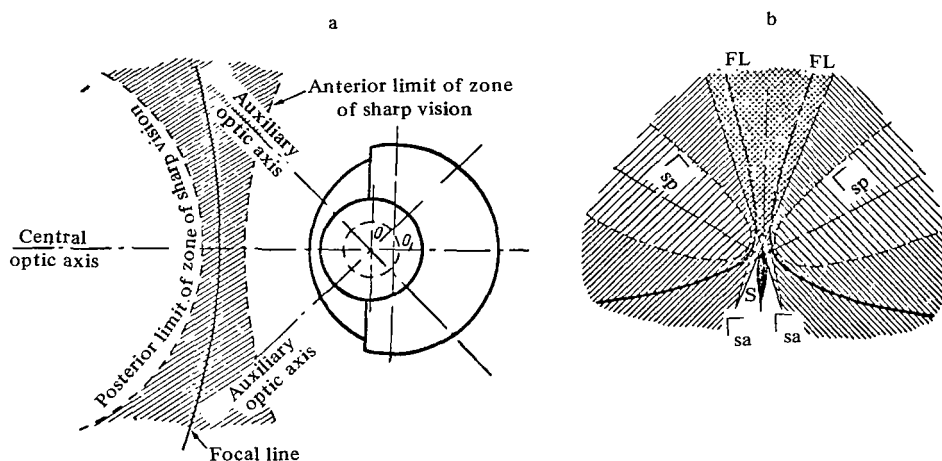


Figure 5. Refraction in a Fish of the Third Type.

a) Diagram of the Refraction of the Fish Eye: 0_1 - Center of the Retinal Hemisphere; 0 - Center of the Crystalline Lens. b) Locational Diagram of the Zone of Sharp Vision. Key as in Fig. 3b.

This arrangement of the zones of sharp vision in the eel and the trout is in full agreement with the features of their ecology. It should be noted that these two species are predators.

Thus, for example, the trout makes active use of its sight in the pursuit of prey and often seizes its prey in the air, leaping to the surface in pursuit of flying insects. A considerable role is naturally played in this by the capacity of its eye to focus sharply on objects a considerable distance in front. It should also be noted that all objects located directly in front of its head are in the field of binocular vision and simultaneously in the zone of sharp vision of its eyes, which is of considerable assistance to the trout in precisely judging the distance of the leap to a target in the air.

The following brief conclusions may be drawn from all that has been said concerning the types of refraction of the fish eye.

The overwhelming majority of the eyes of the fishes investigated by us, with the exception of some benthophages, simultaneously exhibit all three forms of refraction: myopia, emmetropia and hyperopia.

Such a phenomenon, which has the effect that the eyes of the fishes have simultaneous differential focussing for sharp vision of objects separated in space

at different viewing angles to the central optic axis has not previously been discovered in any order of creatures living on the Earth and may clearly be of some interest to optical specialists for its bearing on the design of optical equipment employing data on the structure and functioning of the eyes of some fish species.

It seems to us that the arbitrary division of all fish eyes into three types is merely tentative and that the concept of the types of eyes will be considerably extended as there is further study of the structure and 3-dimensional elements of the eyes of different species of freshwater and marine fishes.

REFERENCES

1. Andriyashev, A.P. Tr. soveshch. ikhtiologich. komissii AN SSSR. (Conference Proceedings of the Ichthyological Commission, USSR Academy of Sciences), 6, 135, 1955.
2. Gal'perin, A. Glubina rezko izobrazhayemogo prostranstva pri kino- i fotos'yemke (The Depth of a Clearly-Depicted Space in Cinematography and Photography). Iskustvo, Moscow, 1958.
3. Lapauri, A.A. Fotograficheskaya optika (Photographic Optics). Iskustvo, Moscow, 1955.
4. Manteyfel', B.P. Tr. inst. morfologii zhivotnykh AN SSSR (Proceedings of the Institute of Animal Morphology, USSR Academy of Sciences), 39, 5, 1961.
5. Morozova, T.Ye. Dokl. AN SSSR, 28, 4, 73, 1951.
6. Romeys, B. Techniques in Microscopy (Translation into Russian). For. Lit. Press, Moscow, 1953.
7. Baylor, E. and E. Shaw. Science, 136, 157, 1962.
8. Beer, T. Arch. f. d. ges. physiol., 58, 523, 1894.
9. Hess, C. von Vergleichende Physiologie des Gesichtssinnes (Comparative Physiology of Vision). In: Handbuch der vergleichenden Physiologie (Handbook of Comparative Physiology). Ed. Winterstein. 4, 1, Jena. Gustav Fischer, 1912.
10. Meader, R. Yale Journ. Biol. and Med., 8, 511, 1936.
11. Pincher, C. A Study of the Fish, London, 1947.
12. Tamura, T. Bull. Japan Soc. of Sci. Fish, 22, 12, 1957.
13. Walls, G. The Vertebrate Eye and Its Adaptive Radiation. Cranbrook Inst. of Science, Bull. No. 19, 1942.

Institute of Animal Morphology,
USSR Academy of Sciences

HISTOCHEMICAL HETEROGENEITY OF RETINAL NEURONS EXEMPLIFIED BY DISTRIBUTION OF ACID PHOSPHATASE ACTIVITY

M. A. Ostrovskiy and S. Ye. Polyak

The distribution of acid phosphatase activity in the frog retina was investigated histochemically in relation to functional differences in retinal neurons, and especially in cells of the inner nuclear layer. Deposits of lead sulfide, indicating the presence of enzyme activity, are clearly seen in the ganglion cells and in Mueller's fibers, and also in the horizontal cells of the inner nuclear layer. Practically no deposition of lead sulfide was observed in the bipolar cells of this layer or in the photoreceptors.

Recent electrophysiological investigations have given a detailed picture of the characteristics of responses of different retinal cells, especially cells of the inner nuclear layer [1]. Histochemical [6, 7] and structural [14] differences between the cells of this layer — bipolar, horizontal, and amacrine cells — have also been established. /155

The writers have made a histochemical study of the localization of acid phosphatase (pH 5.0) activity in the cells of the frog retina. This enzyme is a nonspecific phosphomonoesterase and it participates in hydrolysis and in the transfer of phosphate groups, and in all probability also in protein metabolism and conversions of RNA [2].

Both acid and alkaline phosphatases have been demonstrated biochemically in the retina, but mainly the alkaline enzyme has been determined histochemically [8, 10-13, 16].

METHOD

Acid phosphatase in the intact retina of the frog Rana temporaria was demonstrated by Gomori's improved method [5, 9] with certain modifications.

Immediately after its removal from the optic cup the retina was fixed for 30-45 min in cold calcium-formol solution, after which it was washed and immersed in an incubation mixture ($t = 37^{\circ} \text{C}$, $\text{pH} = 5.0$, incubation time from

30 min to 3 h). After incubation the retinas were treated for 30 sec or 1 min with 1% sodium sulfide solution and then washed and fixed in cold neutral 5% formalin. The material was mounted in gelatin. In the control the retinas were incubated in medium without substrate (β -glycerophosphate). Transverse sections of the retinas were cut and the localization of acid phosphatase activity in them was determined from the deposits of black lead sulfide.

EXPERIMENTAL RESULTS

Deposits of lead sulfide in the frog retina were seen particularly clearly in the ganglion cells, which are typical neurons (Figs. 1a, 2).

In the inner plexiform layer, the glial fibers of Mueller can be seen very clearly as they run across the layer transversely, showing as a broken line of deposited granules (Figs. 1a; 3a, b). Sometimes they are twisted (Fig. 3a). Plexuses of nerve fibers can be seen running along this same layer of the frog retina in sections impregnated with silver by the Gros—Bielschowsky—Lavrent'yev method [3]. Frequently branching fibers of this type, in sections tested for acid phosphatase, are strongly stained (Fig. 3a). This correlates with the results obtained by several workers which indicate a positive reaction of the nerve fibers for acid phosphatase [4].

/156

The character of deposition of lead sulfide is different in cells of the inner nuclear layer, which consists of a mass of bipolar cells transmitting impulses from the receptors in a centripetal direction and also, in all probability, of associative elements—the horizontal and amacrine cells.

The amacrine cells of frogs are larger than the bipolars and they lie on the border with the inner plexiform layer, to which they give off their processes. Considerable deposition of lead is visible in the nuclei of these cells (Fig. 3c). A similar deposit is also found in the large and small pear-shaped cells that can be seen to be displaced into the inner plexiform layer (Fig. 3b). These may be either microglial cells or Dogiel's cells, or cells belonging to the amacrine type.

Bipolar cells throughout the inner nuclear layer, even after prolonged incubation, as a rule exhibit only a diffuse, brownish-yellow background coloration, virtually free from granules of deposited lead sulfide.

The horizontal cells in the frog retina are slightly flattened and are arranged evenly at the boundary between the inner nuclear and outer plexiform layers (Figs. 1a, 2). Their nuclei fill nearly the whole cell, leaving only a thin border of the perikaryon.

The lead sulfide deposits in these cells are very considerable and can be compared only with those in the ganglion cells. Granules of the deposit can also be seen in the nuclei of these cells after incubation for comparatively short times (30 min-1 hr), and after long periods (3 hr) the cells become almost black and their cytoplasm cannot be examined. No deposit is observed in the photoreceptors (Fig. 1a).

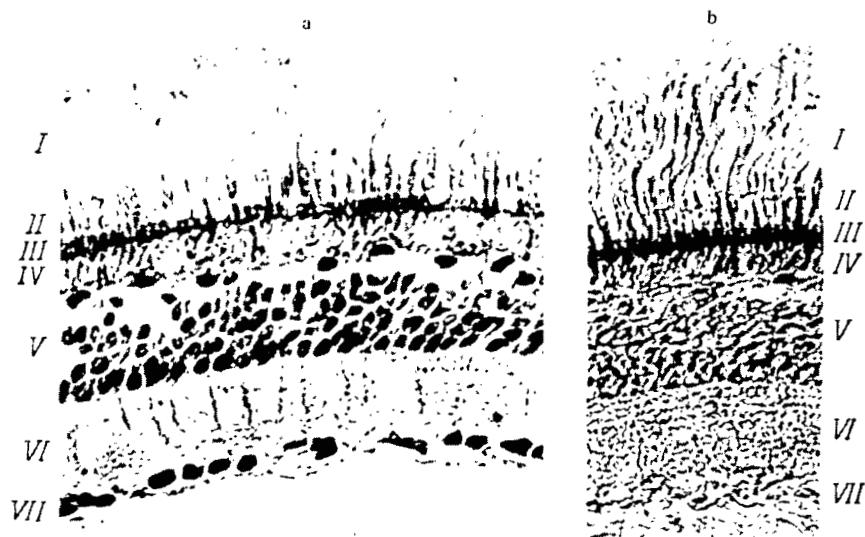


Figure 1. Photomicrograph of Frog Retina.

a - Distribution of Lead Sulfide Deposit in Retinal Cells after Staining for Acid Phosphatase by Gomori's Method [9], $200\times$; b - Nonspecific Deposition of Lead Salt on Outer Limiting Membrane in Control Test, $200\times$. Here and in Figs. 2 and 3 Retinal Layers are Designated: I - Layer of Photoreceptors; II - Outer Limiting Membrane; III - Outer Nuclear Layer; IV - Outer Plexiform Layer; V - Inner Nuclear Layer; VI - Inner Plexiform Layer; VII - Layer of Ganglionic Cells.

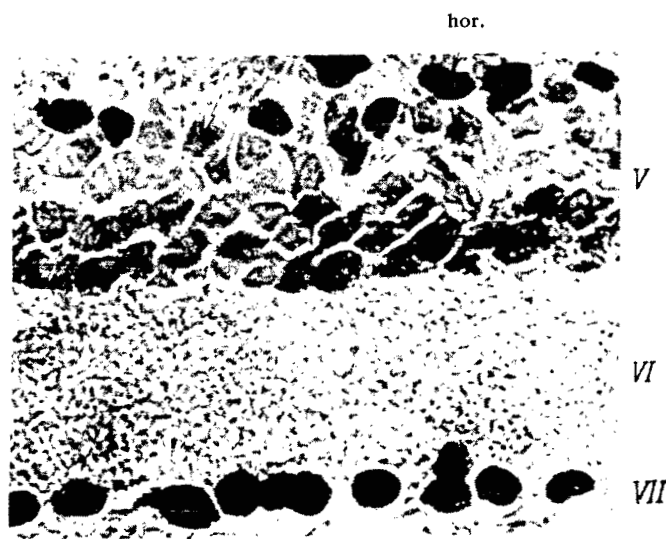


Figure 2. Photomicrograph of Frog's Retina ($450\times$). Marked Deposition of Lead Sulfide in Ganglion (Gang.) and Horizontal (Hor.) Cells. Only Diffuse Staining in Bipolar (b) Cells.

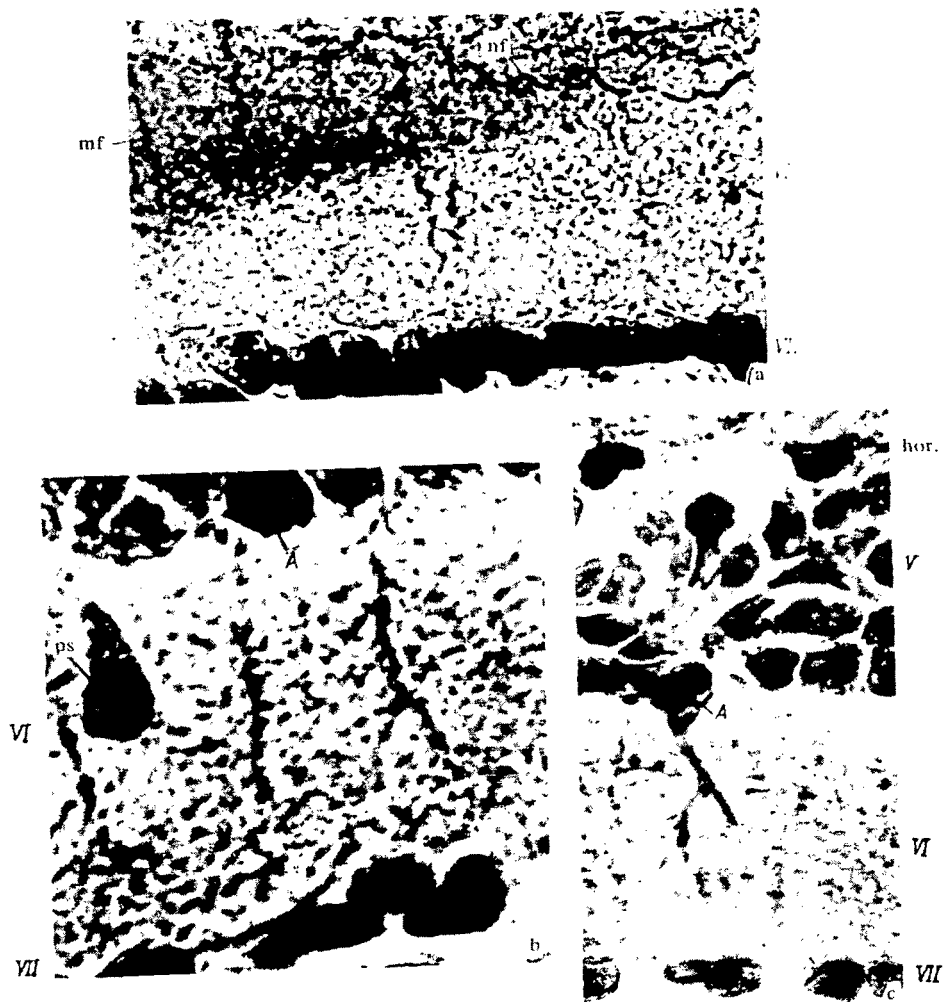


Figure 3. Photomicrograph of Frog Retina (450 \times).

a - Deposition of Lead Sulfide in Mueller's (mf) and Nerve (nf) Fibers of Inner Plexiform Layer; b - the Same in Pear-shaped Cells (ps) and Also in Mueller's Fibers and Amacrine (A) and Ganglion Cells; c- the Same in Cells with Branching Processes (? Amacrine Cells) and also in Horizontal (Hor.) and Ganglion Cells.

Along the outline of the outer limiting membrane there is a dark brown band, forming the background coloration (Fig. 1a).

A well-marked band of deposit can also be seen in the control sections (Fig. 1b). According to Newman et al. [15], who studied nonspecific deposition of lead salts in the tissues after staining for acid phosphatase by Gomori's method, deposition of this type is frequently observed on boundary surfaces. This may, perhaps, explain the high affinity of the outer limiting membrane for lead salts. The difference in character of deposition of lead sulfide in the horizontal, amacrine, and neighboring bipolar cells is evidence of the cytochemical heterogeneity of these components of the inner nuclear layer.

The inner nuclear layer of the retina, with its complex functions, is thus divided on the basis of its histochemical features into several types of cells with their particular localization, on the basis of distribution of acid phosphatase activity, and also, as Utina [6, 7] showed previously, on the basis of the RNA content in the cells of this layer.

Enzymochemical differences between the remaining retinal cells — the photoreceptors and ganglion cells — as regards the distribution of acid phosphatase activity are quite pronounced.

It is difficult at present to correlate the biochemical, cytochemical, and electrophysiological features of the nerve cells of the retina. However, in the future, when experimental data have been collected, such a comparison will be possible and will prove useful to the understanding of the essence of neurochemical and neurophysiological processes in different cells of the retina.

/157

REFERENCES

1. Byzov, A.L. *Elektrofiziologicheskiye issledovaniya setchatki* (Electrophysiological Investigations of the Retina), Nauka Press, Moscow, 1966.
2. Dixon, M. and E.C. Webb. *Enzymes*. Longmans, London, 1958.
3. Ostrovskiy, M.A. *K voprosu o niskhodyashchikh vliyaniyakh na setchatku glaza amfibi* (Descending Influences on the Amphibian Retina), Moscow, 1962.
4. Fortunatov, V.V. *Ocherki gistofiziologii nervnykh okanchaniy* (Outlines of the Histophysiology of Nerve Endings), Medgiz, Moscow, 1955.
5. Pearse, A.G.E. *Gistokhimiya* (Histochemistry). Foreign Lit. Press, Moscow, 1962.
6. Utina, I.A. *Biofizika* (Biophysics) 5, 626, 1960.
7. Utina, I.A. *Dokl. Akad. Nauk SSSR* 157, 1216, 1964.
8. Allen, R.S. and I.S. Friedenwald. *Arch. Ophthalmol.* 50, 671, 1953.
9. Gomori, G. *Arch. Path.* 32, 189, 1941.
10. Joshida, M. *Japan J. Physiol.* 7, 190, 1957.
11. Joshida, M. *Japan J. Physiol.* 7, 195, 1957.
12. Joshida, M. *Japan J. Physiol.* 8, 31, 1958.

13. Lindeman, V.F. Proc. Soc. Exp. Biol. Med., New York, 71, 435, 1949.
14. Meller, K. and P. Echnner. Z. Zellforsch. 64, 733, 1964.
15. Newman, W., E. Kabat and A. Wolf. Amer. J. Path. 26, 489, 1950.
16. Vincentis, M. and M. Tester. J. Histochem. Cytochem. 7, 393, 1959.

Institute of Higher Nervous Activity and Neurophysiology,
Academy of Sciences of the USSR

A STUDY OF THE FUNDUS OCULI IN POLARIZED LIGHT

R. M. Tamarova

The present paper contains a description of the operational principle of two polarization instruments, an apparatus to photograph the fundus oculi [3] and a "maculotester", an instrument for subjective investigation of the macula retinae [4]. Data obtained by means of these instruments prove existence of areas having different forms of optical anisotropy in the fundus oculi.

Polarization methods have found ever-increasing application in biological and medical research during the last few years. The phenomena of optical anisotropy discovered in polarized light provide an indication of the internal structural features of the tissues and are most important characteristics of them.

/158

Although biomicroscopy of the eye in polarized light is a comparatively recent development, the success achieved in the first studies [2, 6] has shown that this method is extremely valuable in study of the fine structure of the transparent media of the eye under normal and pathological conditions and that it may be used for diagnostic purposes. The lack of special instruments has hitherto precluded investigation of the fundus oculi in polarized light.

Optical anisotropy of the tissues of the fundus oculi has been detected only from the phenomena subjectively observed by the subject himself, the best investigated of which is Haidinger's phenomenon [1, 7]. The essence of Haidinger's phenomenon or "brush" is that on looking at a field uniformly illuminated by polarized light the eye sees a weak dark figure in the form of two eroded sectors converging at a point corresponding to the center of the macula retinae.

Many hypotheses have been advanced to account for Haidinger's phenomenon. Dichroism and birefringence of the tissues of the fundus oculi and of the transparent media of the eye have been suggested. Nevertheless, it has not hitherto been possible to obtain objective confirmation of the existence of the presumed structures of the macula retinae.

This led the well-known physicist Raman to advance a new hypothesis rejecting any physical basis for Haidinger's phenomenon and explaining the phenomenon by the purely physiological perception of polarized light.

The present paper contains a description of the operational principle of two polarization instruments, an apparatus to photograph the fundus oculi [3] and a "maculotester", an instrument for subjective investigation of the macula retinae [4], both developed under the author's direction at the All-Union Research Institute for Medical Instrument Making (VNIIMP). Data obtained by means of these instruments are given: these data prove the existence of areas having different forms of optical anisotropy in the fundus oculi.

An optical model of the macula retinae incorporating all the observed phenomena, including Haidinger's phenomenon, is proposed on the basis of these data.

EXPERIMENTAL SECTION

/159

The main experiments were carried out on an apparatus for photographing the fundus oculi. The optical elements of the apparatus are shown in Fig. 1.

It was found in working with the apparatus that the illuminance and color shades in the image of individual portions of the fundus oculi were subject to perceptible variation in relation to the direction of the axes of the crossed polaroids. These phenomena were strongly pronounced in some eyes and only slightly in others. The pattern of the main portion of the fundus oculi was the same in appearance as when examined in non-polarized light.

The most perceptible changes were those in the region of the optic disk. When one of the crossed polaroids was parallel to the large vessels running upward and downward from the optic disk, the areas of tissue around these vessels were red and indistinguishable from the other areas of the fundus oculi. When the polaroids were rotated by 45° these areas became lighter and acquired a yellowish color.

Alteration of brightness and coloration when the polaroids were rotated by 45° was also noted in some pathological foci. In some instances even the apparent limit of the focus was altered.

Figures having the appearance of an eroded yellowish cross on a red background were sometimes observed in the peripheral areas of the fundus oculi. These figures rotated on rotation of the polaroids. The light arms of the cross ran parallel to the axes of the crossed polaroids (Fig. 2). Alternation of the maxima and minima of illuminance in the light figure therefore takes place at intervals of 45° .

In the central area, the region of the macula retinae, the appearance of the light figure was different in all the eyes examined. In it there were two dark bundles on a lighter ground instead of the four in the instances described above. In this figure, therefore, the alternation of dark and light areas occurs at intervals of 90° , not 45° . No such figure was observed in any other area of the fundus oculi.

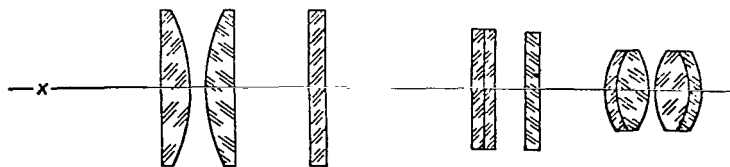


Figure 3. Optical Arrangement of the Polarization Maculotester. Explanations in Text.

THE OPTICAL MODEL OF THE MACULA RETINAE

In order to determine the form of optical anisotropy, the sequence of arrangement of the anisotropic layers and the orientation of the anisotropic elements from the nature of the observed pattern, the author calculated the intensity distribution of the emerging light on passage through different combinations of optically anisotropic layers and found those combinations which produced a pattern identical to that obtained in the experiment.

It was assumed on the basis of the experimental results that the bulk of the light was depolarized on diffuse reflection from the fundus oculi. It was borne in mind that the light passed through each layer twice, incoming and outgoing, and that the optical axis of the layer for the incoming rays was a mirror image of the axis for the outgoing rays. Thus, if the angle between the optical axis and the horizontal for the incoming rays was α , the angle for the outgoing rays was $-\alpha$.

Matrix methods of calculation were used in view of the cumbersome and laborious nature of trigonometric calculations in the penetration of a large number of layers. Since the layer system contains scatterers which depolarize light falling on them, we selected from these methods the method of Muller, which enables a depolarizer to be introduced into the matrix system.

In this method a light beam is described by a Stokes' vector defined by the four parameters I, M, C and S. The parameter I characterizes the intensity of the light and the parameters M, C and S are respectively the parameters of the preferential horizontal polarization, the preferential polarization at an angle of 45° and the preferential right-hand polarization.

The Stokes' vector for the different forms of polarized light and also the basic standard matrices for the different elementary anisotropic components are given in the paper by W. Sheercliff [5]. The matrices of a polarizer with arbitrary azimuth not given in this paper were calculated by means of the matrices of rotation.

The hypothesis explaining Haidinger's phenomenon by the dichroism of radially arranged retinal fibers in the region of the macula retinae and by the birefringence of the retinal receptors was therefore verified in the following manner. The vector of horizontally polarized light falling on the eye was multiplied by the matrix of the dichroic matter (the tissue of the macula retinae), the

matrix of the birefringent matter (receptors), the matrix of the depolarizer (the deeper-lying layers of the fundus oculi) and then by the matrices of the same media through which the light passed on the return journey of the rays, and by the matrix of the analyzer incorporated in the instrument.

For the area with horizontally oriented dichroic elements we obtain:

$$\begin{aligned} & \frac{1}{8} \begin{bmatrix} 1 & -1 & 0 & 0 \\ -1 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix} \begin{bmatrix} k_1 + k_2 & k_1 - k_2 & 0 & 0 \\ k_1 - k_2 & k_1 + k_2 & 0 & 0 \\ 0 & 0 & 2\sqrt{k_1 k_2} & 0 \\ 0 & 0 & 0 & 2\sqrt{k_1 k_2} \end{bmatrix} \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & \cos \delta & -\sin \delta & 0 \\ 0 & \sin \delta & \cos \delta & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix} \times \\ & \times \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix} \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & \cos \delta & \sin \delta & 0 \\ 0 & -\sin \delta & \cos \delta & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} k_1 + k_2 & k_1 - k_2 & 0 & 0 \\ k_1 - k_2 & k_1 + k_2 & 0 & 0 \\ 0 & 0 & 2\sqrt{k_1 k_2} & 0 \\ 0 & 0 & 0 & 2\sqrt{k_1 k_2} \end{bmatrix} \begin{bmatrix} 1 \\ 0 \\ 0 \\ 0 \end{bmatrix} = \\ & = \frac{k_1 k_2}{2} \begin{bmatrix} 1 \\ -1 \\ 0 \\ 0 \end{bmatrix} \end{aligned}$$

The vector obtained describes vertically polarized light of intensity $I = \frac{k_1 k_2}{2}$, where k_1 and k_2 are the principal transmission values of the dichroic matter and δ is the phase shift in the refracting layer.

For the area with elements oriented at an angle of 45° , we replace in the product the matrix

$$\begin{bmatrix} k_1 + k_2 & k_1 - k_2 & 0 & 0 \\ k_1 - k_2 & k_1 + k_2 & 0 & 0 \\ 0 & 0 & 2\sqrt{k_1 k_2} & 0 \\ 0 & 0 & 0 & 2\sqrt{k_1 k_2} \end{bmatrix}$$

describing the horizontally oriented dichroic elements by the matrix

$$\begin{bmatrix} k_1 + k_2 & 0 & -k_1 + k_2 & 0 \\ 0 & 2\sqrt{k_1 k_2} & 0 & 0 \\ -k_1 + k_2 & 0 & k_1 + k_2 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix},$$

describing the dichroic elements oriented at an angle of 45° to the horizontal, and obtain

$$I = \frac{(k_1 + k_2)^2}{8}.$$

For the area with vertically oriented elements, we substitute the matrix

$$\begin{bmatrix} k_1 + k_2 & -k_1 + k_2 & 0 & 0 \\ -k_1 + k_2 & k_1 + k_2 & 0 & 0 \\ 0 & 0 & 2\sqrt{k_1 k_2} & 0 \\ 0 & 0 & 0 & 2\sqrt{k_1 k_2} \end{bmatrix}$$

and obtain

$$I = \frac{k_1 k_2}{2}.$$

Intensities are found similarly for areas with different angles of inclination of the fibers.

Comparison of the results obtained shows that the intensity of the outgoing light varies from maximum to minimum through 45° and that a cross-shaped figure should develop in the field of vision. The same results are obtained with any other combinations of layers.

/162

Therefore, the passage of light through a set of ordinary optical anisotropic layers may give rise to the phenomena observed in crossed polaroids in the peripheral areas of the fundus oculi, but cannot give rise to the phenomena observed in the region of the macula retinae.

In order to produce a model of the macula retinae reproducing the phenomena observed in crossed polaroids and also Haidinger's phenomenon, we made the assumption that light travels in only one direction through some one of the anisotropic layers. Such a case may be imagined if the anisotropic layer is in the form of a lattice, i.e., if the space between the homogeneous anisotropic elements is filled with elements not possessing anisotropy. Such an assumption is not at variance with the anatomical structure of the tissues of the fundus oculi.

In that case a part of the luminous flux entering between the anisotropic elements of the lattice will pass back through its elements. This part of the flux is assumed to be dominant.

The distribution of the outgoing light for this part of the flux with a "reticulate" layer of dichroic, radially arranged elements and a layer of birefringent elements is determined from the following products. For an area with horizontally oriented dichroic elements

$$\frac{1}{8} \begin{bmatrix} 1 & -1 & 0 & 0 \\ -1 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix} \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & \cos \delta & -\sin \delta & 0 \\ 0 & \sin \delta & \cos \delta & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix} \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & \cos \delta & \sin \delta & 0 \\ 0 & -\sin \delta & \cos \delta & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix} \times$$

$$\times \begin{bmatrix} k_1 + k_2 & k_1 - k_2 & 0 & 0 \\ k_1 - k_2 & k_1 + k_2 & 0 & 0 \\ 0 & 0 & 2\sqrt{k_1 k_2} & 0 \\ 0 & 0 & 0 & 2\sqrt{k_1 k_2} \end{bmatrix} \begin{bmatrix} 1 \\ 1 \\ 0 \\ 0 \end{bmatrix} = \frac{k_2}{2} \begin{bmatrix} 1 \\ -1 \\ 0 \\ 0 \end{bmatrix}$$

The intensity of the outgoing light is $I = \frac{k_2}{2}$.

For an area with vertically oriented elements we similarly obtain $I = \frac{k_1}{2}$.

Comparison of the intensities obtained for different k_1 and k_2 shows that the alternation of intensity maxima and minima of the outgoing light occurs at intervals of 90° and that the figure which develops in the field of vision is in the form of two dark bundles on a light background, identical to the figure observed in the experiment.

The combination of layers under consideration also reproduces Haidinger's phenomenon. Similar results are yielded by a combination of a "reticulate" optically anisotropic layer and some other optically anisotropic layers.

Therefore, the figure observed in the region of the macula retinae may be reproduced in a model consisting of optically anisotropic layers. At least one layer in this model should consist of radially directed dichroic elements and at least one layer should have a "reticulate" structure.

CONCLUSIONS

/163

1. When the fundus oculi is examined in crossed polaroids uneven distribution of light intensity is noted in a number of areas; this intensity varies in relation to the direction of the axes of the polaroids, thus proving their optical anisotropy.

2. The nature of the pattern which develops is different for the central area of the fundus oculi, the macula retinae, and for its other areas. In the region of the macula retinae light intensity varies from maximum to minimum on rotation of the polaroids by 90° ; in all other areas this variation occurs on rotation by 45° .

3. The optical model proposed for the macula retinae, which has a reticulate optically anisotropic layer, reproduces the alternation of maxima and minima of light intensity observed in crossed polaroids when the direction of the polaroid axes is varied by 90° .

This model reproduces the optical phenomena observed in the region of the macula retinae when investigated with a single analyzer and also Haidinger's phenomenon.

REFERENCES

1. Brumberg, Ye.M. and P.P. Feofilov. Dokl. AN SSSR, 22, 3, 1941.
2. Smirnov, A.A. Biofizika (Biophysics), 8, 6, 1963.
3. Tamarova, R.M., T.N. Myagkikh, B.I. Ushakov and V.I. Kiryukhin. Apparat dlya fotografirovaniya glaznogo dna (An Apparatus to Photograph the Fundus Oculi), Inventor's Certificate No. 145447, dated 19 November 1962.
4. Tamarova, R.M., V.M. Dolbishcheva and B.I. Ushakov. Pribor dlya issledovaniya zheltogo pyatna setchatki (An Instrument to Examine the Macula Retinae), Inventor's Certificate No. 171964 dated 21 June 1965.
5. Sheercliff, W. Polarized light (translation into Russian). Mir Press, Moscow, 1965.
6. Saüchi Mishima. Advances in Ophthalmology, Ed. E. B. Streiff, Lausanne, 1960.
7. Forster, H.W. Amer. Journ. Ophthalmol., 38, 250, 1954.

All-Union Scientific Research Institute of Medical Instrument Making

USE OF POLARIZED LIGHT TO STUDY THE ANATOMY, PHYSIOLOGY, AND PATHOLOGY OF THE FUNDUS OCULI

D.I. Mitkokh

Analysis of the results of an ophthalmoscopic study of 60 patients using an apparatus with built-in polaroids to inspect and photograph the fundus oculi. It is found that the structure of the fundus oculi (in particular, the macula lutea) is more easily visible in polarized light, thus facilitating early diagnosis of various diseases of the optic nerve and the macula lutea. It is also noted that by varying the position of the polaroids it is possible to obtain both black-and-white and color photographs of the fundus oculi.

Methods and instruments used at the present time for ophthalmoscopy are not always suitable for studying the complex structure of the fundus oculi and the changes developing in disease.

/164

The writer, in conjunction with R.M. Tamarova, has developed a new method of investigating the fundus oculi [4, 5]. Ophthalmoscopy is carried out with a Soviet instrument for photographing the fundus oculi, fitted with revolving polaroids. Tests carried out in polarized light have shown that the tissues of the fundus oculi possess optical anisotropy in the form of dichroism and birefringence.

Investigation of the fundus oculi in polarized light was carried out in the eye clinic of the M. F. Vladimirskiy Moscow Clinical Research Institute (Clinic Director Professor D.A. Berezinskaya). Altogether 150 eyes were tested. The number of eyes tested in healthy persons and in patients with various eye diseases is indicated below.

Healthy eyes	36
Acquired diseases affecting	
a) the optic nerve	16
b) the macula lutea of the retina	45
c) vessels of the fundus oculi	11
Congenital changes affecting the fundus oculi	8
Neoplasms of the fundus oculi	8
Other diseases	11
Recurrent diseases	15
Total	150

Inspection of the fundus oculi of the healthy persons showed that during rotation of the polaroids the chromaticity and brightness of the tissues of the fundus oculi are modified, reflection is intensified around the blood vessels, and the optic disk and macula lutea are more clearly outlined. The borders of the optic disk appear particularly distinct, and a clear view is obtained of the surrounding rim of sclera, the vessels leaving the papilla of the optic nerve, and nerve fibers surrounding the vessels, which cannot be seen with existing methods of investigation. In the region of the macula lutea on rotation of the polaroids the central fovea and its reflection can be clearly differentiated. If pigmentation in the fundus oculi is normal, the intact retina is difficult to distinguish from the pathological. In cases when there is little pigment, it is clearly visible in polarized light. By rotating the polaroids, the tissue located beneath the pigment can be examined. In just the same way, by using revolving polaroids, the membranes of the fundus oculi can be distinguished layer by layer: the retina and the vascular membrane, an extremely important matter when the optic fundus is studied under normal and pathological conditions.

In the region of the macula lutea (if it is intact), a dark red figure resembling two triangles connected by their apices at the fovea centralis appears on rotating the polaroids. The figure revolves as the polaroids are rotated and can be clearly seen in persons with a normal fundus oculi. In young subjects the figure is more clearly visible. Differences in the intensity of coloring of the figure under normal conditions are perhaps dependent on the quantity of yellow pigment in the macula. In the albino, for instance, when the macula lutea is intact, the polarized figure is very pale. In its shape, size, and localization, the figure described corresponds to Heideringer's figure, which previously could be observed only subjectively as an entoptic phenomenon. /165

There is, of course, as yet no unanimity regarding the nature of the mechanisms of Heideringer's phenomenon.

During objective investigation of the fundus oculi in polarized light, such a figure appears only in the region of the macula lutea and its configuration is due to the anatomical structure of the macula lutea.

Changes in the chromaticity and brightness of the fundus oculi also made it possible to diagnose lesions of the optic nerve in an early stage, when changes in the fundus oculi are difficult to detect by ordinary tests. In partial optic atrophy, the characteristic brightness appears very early around the optic disk and the nerve fibers surrounding the large blood vessels. If the polaroid is rotated slight pallor of the optic disk in some parts becomes visible. In neuroretinitis of varied etiology, precapillary edema is clearly visible. In the presence of changes in chromaticity and brightness, the optic disk is precisely differentiated, and because of this its boundaries and any changes taking place in it can be clearly examined.

Investigations of patients with various lesions of the macula lutea (central chorioretinitis, maculitis, degeneration of the central parts of the retina, hemorrhage in the region of the macula, and so on) have shown that the polarization figure described above is a valuable diagnostic and prognostic sign. The

clarity of the figure depends on changes taking place in the macula in different diseases. One reason for absence of the figure may be marked edema in the region of the macula. In such cases, periodic examination of the patient will reveal the polarization figure when the edema disappears. Under these circumstances, appearance of the figure will precede an improvement in visual function. Objective investigation of the fundus oculi in polarized light can thus be used to test the effectiveness of treatment.

The writer has developed and used for clinical purposes a combined method of investigation of the polarization properties of the fundus oculi [1, 2, 3]. To begin with a subjective investigation is carried out using the maculotester. Then, depending on the results of this test, the patient is subjected to an ophthalmoscopic examination using an apparatus for photographing the fundus oculi, equipped with revolving polaroids. If necessary, the fundus oculi is photographed in polarized light [1]. If the result of the subjective test is negative, sometimes a polarization figure is observed objectively in the region of the macula. Subjective observation of the figure in such cases may be prevented by the following factors: 1) the presence of a central scotoma; 2) the absence of central fixation; 3) the subject's low intellect; 4) edema in the region of the macula.

These factors do not prevent the examiner from seeing the polarization figure in the patient's fundus oculi.

Objective investigation of the fundus oculi in polarized light frequently helps to make a more precise diagnosis of the disease. For example, in a patient with juvenile degeneration of the central part of the retina, ophthalmoscopy in polarized light revealed secondary optic atrophy. This could be done because, on rotating the polaroids, decoloration of the optic disk and flattening of its temporal part became visible. The latter was evidence of a lesion of the papillomacular bundle. The polarization figure in the region of the macula did not appear on rotating the polaroids. It was concluded from these tests that the papillomacular bundle was involved in the disease in a patient with degeneration of the macula, and as a result he developed secondary optic atrophy.

/16

During investigation of the blood vessels of the fundus oculi in polarized light, a reflected band on the vessels can be observed from time to time. If the polaroids are rotated through 45° , the reflected band may disappear or attain maximum intensity.

If the vessel walls become sclerosed, the main source of reflection becomes the wall itself. In these cases the width of the reflected band depends on thickening of the vessel wall, and brightness of the reflection depends on its degree of degeneration. Tests carried out by the writer showed that during progression of sclerotic changes in the vessels the reflected band become wider and more distinct, and the outlines of the vessel walls clearer. On rotating the polaroids, unevenness of the reflected band becomes clearly visible, and in the places where the vessel wall is thickened the band becomes wider and brighter. Consequently, periodic examination of the reflected band on the vessels makes it possible to diagnose the degree of severity of sclerosis of the blood vessels.

Among the patients with congenital changes in the fundus oculi who were tested, most had well-marked pathological changes (most frequently a coloboma of the choroid, choroidal foci, etc.). In such patients, on rotation of the polaroids, the chromaticity and brightness of the fundus oculi were almost unchanged in the region of the foci. The explanation of this may be that, because of gross changes (development of connective tissue), optical anisotropy, usually characteristic of the tissues of the fundus oculi, was not apparent. The absence of signs of anisotropy in the investigated part of the fundus oculi can therefore be one manifestation of congenital or chronic changes.

Patients with neoplasms were investigated in polarized light in order to establish the precise location of the focus in the fundus oculi. Tests showed that, depending on whether the interference pattern appearing in certain positions of the polarizer and analyzer is superposed on the pathological focus, or apparently shields it, a decision can be made whether the focus lies behind the transparent anisotropic layer or in front of it. This takes place because of the presence of birefringence in the transparent coats of the eye and it enables the neoplasm (focus) in the fundus oculi to be localized (in the retina or vascular coat).

CONCLUSIONS

1. Investigation of the polarization properties of the fundus oculi was undertaken by two methods: subjective and objective. The subjective method consists of observation by the patient or normal subject of entoptic phenomena arising during the action of polarized light on the retina. This method cannot identify the structures which are responsible for the entoptic phenomena. Objective observation of optical phenomena visible in the fundus oculi enables the question of the nature of these phenomena to be settled.

2. Investigation of the fundus oculi in healthy persons showed that the use of polarized light affords new opportunities for studying the structure of the tissues of the fundus oculi.

/167

3. In the region of the macula lutea, a dark red polarization figure resembling two triangles joined together by their apices in the fovea centralis, has been found for the first time. It was accordingly concluded that Heidinger's figure, visible in the macular region, is a physiological phenomenon connected with the radial arrangement of the nerve fibers in the region of the macula and with their optical properties.

4. Changes in the chromaticity and brightness of other structures in the fundus oculi in polarized light made it possible to diagnose a lesion of the optic nerve (neuritis, atrophy) in the early stage, when changes in the fundus oculi are difficult to find by the ordinary ophthalmoscopic investigation.

5. Tests on patients with various lesions of the macula lutea showed that the polarization figure is a valuable diagnostic and prognostic sign. Absence of the polarization figure is always evidence of a lesion of the tissues in the region of the macula in the retina or of severe edema of the retina in that region. The polarization figure can be used to verify the effectiveness of treatment.

6. During rotation of the polaroids, a reflected band on the vessels can be observed from time to time. The reflected band is more clearly visible on the arteries than on the veins. If the vessel wall becomes thickened, the band becomes more contrasting, wider, brighter, and uneven. It accordingly enables the state of the vessel wall to be judged and the severity of the sclerotic changes in the vessels of the fundus oculi to be diagnosed more accurately.

7. The presence of birefringence in the transparent coats of the eye can be used to localize neoplasms in the fundus oculi (retina, vascular coat). By tests in polarized light it is possible to examine a neoplasm in the fundus oculi layer by layer, thus facilitating the diagnosis of the disease.

REFERENCES

1. Mitkokh, D.I. Trudy V soveshchaniya po fiziologicheskoy optike (Proceedings of the 5th Conference on Physiological Optics) USSR Academy of Sciences, 1966, p. 97.
2. Mitkokh, D.I. Meditsinskaya promyshlennost' SSSR (The Medical Industry of the USSR) 2, 2, 1966.
3. Mitkokh, D.C. Materialy III s'yezda oftal'mologov SSSR (Proceedings of the Third Congress of Ophthalmologists of the USSR) 2, Volgograd, 1966, p. 114.
4. Tamarova, R.M. Trud. Inst. VNIIMIO 1, 128, 1965.
5. Tamarova, R.M. and D.I. Mitkokh. Materialy III s'yezda oftal'mologov (Proceedings of the Third Congress of Ophthalmologists of the USSR) 2, Volgograd, 1966, p. 111.

All-Union Scientific Research Institute of Medical Instrument Making

METHODS OF INVESTIGATING THE ACCOMMODATION TIME IN MAN

A.A. Sychev

The writer has developed a method of studying the accommodation time of the eyes during transfer of fixation from the near distance and also of determining the time of its increase and decrease after fitting optical glasses to the eyes. The instrument incorporates an ordinary TKhP-56-M chronoreflexometer. The use of this method on five subjects showed that the time for de-accommodation after strengthening accommodation by 3.0 D is 0.58-0.69 sec in emmetropes and 0.95-1.11 sec in myopes. The time required for strengthening accommodation by 3.0 D in emmetropes is 1.10-1.20 sec and in myopes 1.07-1.16 sec.

Despite great advances made in the care of eyesight in schoolchildren, the incidence of anomalies of refraction, and especially of myopia, still remains high among this group.

/168

My investigations of the visual acuity and refraction of schoolchildren in Kharkov and of the activity of the visual system in myopic children (5) have convinced me that myopes, unlike emmetropes and hypermetropes, are capable of prolonged visual work at close distances without appreciable signs of fatigue. Analysis of these findings and of data in the literature concerning active accommodation to distance suggests that the myopia of the schoolchild (in mild cases) is evidently an adaptation the result of training of the visual system of schoolchildren to carry out prolonged visual work at a near distance, and, in consequence of this, the result of extinction of the function of active accommodation at a distance.

These considerations have led me to make a more careful and profound study of visual function in schoolchildren, and notably of the whole function of accommodation: its resistance to close work and, more important, the time of accommodation during its strengthening and weakening in individual age groups, and a matter of extreme importance, in association with differences in refraction of the eyes. The time factor is widely used in investigations of various types to assess the function of individual organs or systems, and it was therefore decided to use the time index as the criterion for evaluation of the function of accommodation.

If myopia of mild degree is regarded as the result of reduced function of active distance accommodation, it may be postulated that the force and energy of the act of de-accommodation or of the negative part of its relative range in myopes will be less marked than in emmetropes or hypermetropes.

No information concerning the accommodation time of the human eye during examination of objects located at different distances (during the transfer of fixation), still less in the presence of anomalies of refraction, could be found in the accessible literature. Averbakh [1] points out that a change in accommodation from the resting state to a state of tension requires 0.25-0.5 sec, but this applies only to an increase in the power of accommodation, and it is evidently inaccurate when applied to persons with anomalies of refraction and accommodation.

Information is given in the literature on the rate of perception of depth by pilots [4] and on the time required for evaluation of readings of certain instruments and for orientation in space [3]. However, these investigations tell nothing of temporal responses of accommodation alone, but they are concerned with the duration of activity of the visual system as a whole in trained subjects with considerable experience in their occupations. No methods which could be used to determine the duration of accommodation with a high degree of accuracy likewise could be found in the literature. The method of photoelectric recording of the accommodation reflex [2] is very interesting in this respect, but it also cannot be used to estimate time, for it characterizes only the change in curvature of the anterior surface of the lens.

/169

To study the accommodation time of the eye during the transfer of fixation from a near to a distant object, and also to determine the time of the strengthening and relaxation of accommodation after optical glasses are fitted to the eye (the duration of the positive or negative parts of the relative range of accommodation) the writer devised a special instrument incorporating the ordinary TKhR-50 chronoreflexometer, which can measure the human reaction time with an accuracy of 0.01 sec. The complete apparatus consists of two instruments controlled from a single switchboard.

One instrument is for determining the distant accommodation time. It consists of two separate mechanisms for exposing the objects to be examined, which are different distances away. The screen for presenting the near test object (consisting of two vertical lines, 0.5 mm thick, 0.1 mm apart) is mounted directly on the subject's head-rest on a horizontal platform. This test object can be moved to distances of between 33 and 10 cm from the eye, so that the distant accommodation time can be investigated after an increase in dioptric force of between 3 and 10 D. The second screen for demonstrating a text and its replacement is mounted at a distance of 5 m from the eyes.

The tests are carried out as follows: the subject sits at a table with his head resting on the support. A laryngophone is fixed over his larynx, and the signal from it, during a verbal response (i.e., when reading the test) disconnects an electronic timer. The screen with the test object is placed in front of the subject's eyes at a distance, for example, of 33 m (with emmetropes in this

case the power of accommodation is increased by 3.0 D). This test object is moved away by operation of the instrument, and at a distance of 5 M (on the same line of vision) a text appears for reading (height of the letters 1.0 cm). The electronic timer is switched on simultaneously. As soon as the subject has read the first piece of text, the timer recording the total time of relaxation of accommodation from 3.0 D (in our example) to rest and the duration of the sight-speech reaction is stopped. To determine the true accommodation time, the duration of the sight-speech reaction is investigated there and then, and the differences gives the required value.

The second instrument for determining the energy of the positive or negative parts of the relative range of accommodation (from the time required to increase or decrease the power of accommodation) consists of a mechanism which places 3.0 D concave or convex lenses in front of the eyes and at the same times sets the electronic timer in operation. This mechanism is also mounted on the head-rest. The subject wearing the laryngophone on his larynx and with his forehead resting on the support examines a text of ordinary size at a distance of 33 cm (the power of refraction of an emmetrope is increased by 3.0D). When the mechanism is switched on, the timer begins to work simultaneously, and lenses forcing the subject to strengthen or relax his accommodation are placed in front of his eyes (in our example the use of a 3.0 D biconcave lens requires a total increase in the power of accommodation to 6.0 D). As soon as it becomes possible again to read the text (it is changed at the moment when the mechanism is switched on) and the subject has read the first piece, the timer is stopped. Knowing the time of the sight-speech reaction of the subject at that particular moment, it is easy to determine the true time of increase in the power of accommodation or energy of the positive part of its relative range.

Tests on persons aged 16-25 years showed that consecutive investigations of the rate of increase or decrease in the power of accommodation, and also of the rate of the sight-speech response differ in time by within ± 0.2 sec (after preliminary training). For this reason, it was made a rule in this method of investigation to carry out at least five measurements of the time and then to calculate the mean.

The results of these investigations, performed in their entirety on five subjects (three emmetropes and two myopes) showed that the time of de-accommodation after an increase in its strength of 3.0 D (during the transfer of fixation from a near to a distant object) in emmetropes was 0.58-0.69 sec, compared with 0.95-1.11 sec for myopes. During investigation of the energy of the positive and negative parts of the relative range of accommodation on the second instrument (monocular method, using lenses) in emmetropes the duration of the negative part was 1.16-1.62 sec, and of the positive part (with an increase of power of 3.0 D) 1.10-1.20 sec, compared with 1.10-1.13 and 1.07-1.16 sec respectively for myopes.

/170

To investigate emmetropes and myopes under identical conditions of observation, a correction must be used giving normal vision.

REFERENCES

1. Averbakh, M.I. Oftal'mologicheskiye ocherki (Ophthalmologic Essays) Medgiz, Moscow, 1949, p. 246.
2. Glezer, V.D. and L. T. Zagorul'ko. Fiziol. Zh. SSSR (Physiological Journal of the USSR) 41, 6, 1955.
3. Krasnovidov, V.S. Voën.-Med. Zh (Journal of Military Medicine) 1, 56, 1962.
4. Litinskiy, G.A. Vestn. Oftal'mol. (Ophthalmological News) 12, 6, 1938.
5. Sychev, A.A. Trudy Khar'kovskogo meditsinskogo instituta (Proceedings of The Kharkov Medical Institute) 46, 1958.

Department of Child and Adolescent Hygiene,
Kharkov Medical Institute

THE METHOD OF CONSTANT PERIODS

A. I. Ivanov

The idea behind this method for the determination of visual thresholds stems from the mechanism of sight itself, which reduces in the simplest cases to the temporal and spatial summation of photic stimuli on the retina and the transmission to the brain of signals in the form of discrete, more or less periodic action currents.

A method of threshold measurements has been developed for determination of the characteristics of vision, but it may possibly also be of use in the investigation of other sense organs.

/171

The existing methods for the measurement of visual thresholds are dealt with in manuals of physiological optics [1, 3].

The simplest methods, for example the direct determination of the threshold of visual perception, are not sufficiently accurate in some instances even when there is a large number of observers and readings. This is to be explained by the subjective nature and variability of the criterion of threshold response; to eliminate this subjectivity in ordinary statistical methods the value of the threshold is determined at the same probability of detection (for example 50%), i.e., an objective estimate of the threshold is introduced. However, this requires extremely laborious measurements at several probabilities of detection, including low probabilities, in order to graph the probability of detection as a function of the magnitude of the threshold and to find from the graph a threshold with an assigned probability. With the existing probability methods it is not always possible to carry out examinations and tests which, by their nature, must be completed within a short period. The development of the method of constant periods has accelerated and simplified certain threshold measurements and also the processing of results.

PRINCIPLE AND TECHNIQUE OF THE METHOD OF CONSTANT PERIODS

When a threshold light source producing an illuminance (E) in the pupil appears in the field of vision, the observer does not immediately see a light. At any luminance of the background and given the existence of a fixation point, a period (T) of 10 seconds or more may elapse before the sensation of a short

and definite threshold flash arises and the observer signals to the operator. By increasing the illuminance on the pupil it is possible gradually to reduce the period of detection of the first threshold flash to any quantity down to 0.5 sec (the total reaction time of the operator and the observer in the measurement procedure described below).

There is, therefore, a sufficiently definite relationship between the period (T) (from the recorded time of exposure of the test object to the recorded time of development of a sensation) and the magnitude of threshold illuminance (E). The formula approximating this relationship has been found to be extremely simple:

/172

$$\frac{E_2}{E_1} = \left(\frac{T_1}{T_2} \right)^n, \quad (1)$$

where n is a quantity equal on average to 0.5 (if $2.5 < T < 8$ sec) and independent for point sources of light of the luminance of the background and of the presence of glaring sources of light. This value (1) was obtained by us for 8 observers (see the Table).

Dependence of the Frequency of the Index (n) on its Magnitude

Observer	Magnitude of Index (n)							
	0.3	0.4	0.5	0.6	0.7	0.8	0.9	n_{mn}
1	17	13	8	1	2	—	—	0.40
2	6	9	1	3	1	3	2	0.50
3	5	5	5	4	1	1	1	0.49
4	5	—	1	2	—	—	3	0.54
5	1	1	2	1	—	1	—	0.52
6	1	2	—	—	—	—	—	0.37
7	1	2	—	—	—	—	—	0.37
8	—	—	1	—	1	—	—	0.60

In practice the following measurement procedure was followed. At a preliminary sound the observer fixed his gaze on the fixation point (if one was used) or in the direction known to him where the threshold point light source should appear. After 2—3 sec had elapsed the operator exposed the light source simultaneously with a second short sound signal (or without it) and started the timer. When the sensation of a threshold flash developed the observer pressed a button which lit a bulb in the operator's booth, the operator stopped the timer and recorded the length of the period (T_1). Periods T_2 , T_3 and so on were then found similarly with a stimulus of the same magnitude (E_n).

A single series of readings, consisting approximately of 10 periods, was usually carried out without a break and took several minutes.

In 30% of the readings, at times unknown to the observer the operator gave the ordinary signals without presentation of the light source. The response "I see nothing" was communicated by pressing the signal knob twice. Mistaken responses were noted in the record both in the case "I see" and in the case "I do not see" (see below).

The procedure described above was used in various threshold measurements in which the observed light source was a point source.

Preliminary measurements were also made of the time (T) taken for a large (300') dark figure to appear at twilight-night-time background luminance. Even in this more complicated case, which is an example of the discrimination of details, the periods were found to be sufficiently large (several seconds) for use of the method.

When it had been established (mainly for point light sources) that the periods (T) were sufficiently large and stable for measurement by a timer even at high probabilities of detection, and when the relationship (1) had been established (in the range $2.5 < T < 8$ sec), it became clear that a convenient natural criterion of response had been found for estimation of control of the level of threshold sensation; it had become possible to make the threshold determinate, measuring it wherever possible at the same period (T_0) or converting to this fixed period.

/173

It is evident from expression (1) when $n = 0.5$, i.e., from the formula

$$\frac{E_2}{E_1} = \left(\frac{T_1}{T_2} \right)^{0.5}, \quad (2)$$

that such a method may be adequate for some measurements not requiring great accuracy since, in accordance with [2], slight lack of agreement of the periods when taking readings is comparatively little reflected in the equality of the thresholds. In fact, we have from (2)

$$\frac{\Delta \left(\frac{E_2}{E_1} \right)}{\frac{E_2}{E_1}} = \frac{1}{2} \left[\frac{\Delta \left(\frac{T_1}{T_2} \right)}{\frac{T_1}{T_2}} \right] \quad (3)$$

However, there is a better method to increase the speed and accuracy of measurement: the thresholds E_1, E_2, \dots, E_k are measured without attempting to make the periods equal, i.e., at different periods T_1, T_2, \dots, T_k . Then, using (2), the thresholds are converted to a threshold with the same period T_0 , for example one of 4 sec.

Nevertheless, in order to minimize the effect of inaccuracy in the magnitude of (n), the periods selected should be as close as possible and should not differ by a factor of more than 2, but this does not complicate the experiment.

The method has the considerable advantage over the known methods in speeding up operations in that the threshold levels (E) offered to the observer can be either pre-assigned or even selected by the operator.

Some measurements, for example measurements of the coefficients of blinding, may be made more rapidly and with considerably less stress by the method of equal periods since there is no need to make readings with low probabilities of detection as in probability methods.

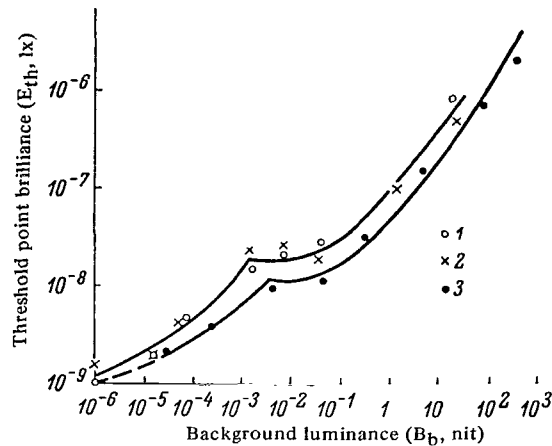
Given the correct choice of period (T), i. e., when the probability is sufficiently high, threshold flashes become certain and the number of incorrect "yes" ("I see") answers is small by comparison with the number of correct "yes" answers, but nevertheless as a check the operator should make approximately 30% of presentations without the test object in the field of vision.

Further increase in the accuracy of the method and simplification of the processing of measurement results became possible when confirmation was obtained of our assumption that the set of first periods (T) of threshold bursts did not have a normal probability distribution. It was shown experimentally to contain a prominent group of identical "true" ("normal") periods with slight dispersion.

It was established that a high percentage of "true" periods falling within a definite range (see below) corresponds to the normal state of vision of the experienced observer and to optimum test procedure (constancy of experimental conditions, established flashes of sensation, not over-large build-up periods T, and training to enable the observer to fix the direction to the test object with sufficient accuracy and without stress and to relax between responses). There are also a number of other conditions which characterize the functioning of an experienced observer and the circumstances of the experiment.

The existence of a tight group of "true" or "normal" periods, which in most experiments covers at least 70% of the readings (some of the others are clearly discardable as mistakes), made possible the next important step in simplification of the recording method and processing of the measurement results: only periods that differ by a factor of not more than 1.5 are processed (averaged). This range was experimentally selected, taking into consideration, in particular, the need to exclude double periods and larger periods treated as gross errors and omissions of the first "normal" period. If two groups of periods are possible, only the group with the smaller period is processed.

The group of periods thus distinguished is averaged and the threshold values are adjusted to a single period (T_0) by equation (2). If necessary the more general equation (1) may be used in order to allow for small differences of (n) in different observers. The quantity n, like the percentage of "true" periods falling within a given range, may be regarded as a measure of the difficulty of the observation conditions in different threshold measurement procedures and as a measure for evaluation of the psychophysiological state and stability of the observer, and also of his proficiency.



The Relationship Between Threshold Point Brilliance (E_{th}) and Background Luminance (B_b). 1, 2) Method of Constant Periods, Series of 10 Periods Per Point. 1 - Measurement No. 1; 2 - Measurement No. 2; 3 - Statistical Method; 2100 Readings of a Point (300 Readings by Each of 7 Observers).

In order to speed up the processing of the results it was found to be very useful to switch from digital recording of period magnitude to the more visual and effective method of entering the readings as lines on logarithmic coordinate paper (horizontal for the response "I see" and vertical for the response "I do not see"; the line for an incorrect response was circled round).

With this method of recording the operator is able to see directly how close are the periods in a given series of readings of an observer, and is able when processing the results to isolate the strongest group of "true" periods fitting into the assigned interval ($T_{max}/T_{min} = 1.5$) if they are entered on logarithmic coordinate paper (merely by running a frame of the appropriate width along the recording).

The method of equal periods has been successfully verified in investigation of the coefficients of blinding, when rapidity of measurement and a definite response criterion are particularly essential. As an example of the rapidity and accuracy of measurement achieved, we give in the Figure the results of measurement of the complex relationship between threshold illuminance on the pupil (E_n) and the background luminance. The relationship was arrived at with an observer employing 8 background luminances in less than 1 hour (2 hours were spent in adaptation). In one experiment the observer carried out two series of readings of 10 periods for each point on the graph, and in another experiment specially conducted to clarify

the possible rapidity of the method, one series of 10 readings (in succession) was even carried out for each background. Despite this, the dependence of E_n on B_b practically coincided with the result of the experiment on 25 August. The maximum deviation from the mean curve was $\pm 12\%$.

The same relationship derived in [2] by the ordinary probability method is given in the Figure for purposes of comparison. Each point was found by averaging 2100 readings (300 readings from each of 7 observers).

Blackwell's threshold values given in the Figure correspond to a probability of detection of 50%. The threshold values found by the method of constant periods (see the Figure) were determined at a probability of 80%. If necessary they could be converted by known formulas to a probability of 50 or 75% [1].

According to a provisional estimate, the magnitude of the coefficient of variation is considerably less with this measurement method than with the other known methods:

$$V = \frac{\sigma}{E_n} \approx 0.2$$

for a set of thresholds of detection (E_n) of a point source observed against the same background in different experiments carried out at intervals over 20 days. In experiments of short duration the coefficient of variation of the measurement method under consideration will be less than the stated value since the probability of large fluctuations in the threshold sensitivity of the observer is not so great as in measurements covering a number of days.

For example, for experiments lasting 2–3 hours, $V_{mn} \approx 0.1$, while for experiments lasting 3–5 min $V_{mn} \approx 0.05$ if the observer had experience with the method.

The last value of V was determined by the formula

$$V = \frac{\sqrt{\sum_1^N \left[1 - \left(\frac{T_{mn}}{T_c} \right)^n \right]^2}}{N - 1}$$

for a set of thresholds (E_i) calculated by (1) for a group of "true" periods of one series from $N = 7$ –10 readings with a constant stimulus.

The provisional values of the coefficient of variation of threshold sensitivity here given demonstrate the advantages of the method, namely the possibility of carrying out the entire investigation with a smaller number of readings and in a shorter time, the effect of which is fuller elimination of the distorting effect on the relationships under investigation both of temporal variations and of the drift of threshold sensitivity.

CONCLUSIONS

1. The method of constant periods which has been developed eliminates subjectivity of response in threshold measurements by establishing the duration of the period of the first threshold flash of perception.

2. The relationship (1) between the magnitude of the threshold (E_n) and the period of the flash (T) experimentally established in the range $2.5 < T < 8$ sec makes it possible to obtain all thresholds with an identical period (T_0).

3. Provided that certain observation conditions are observed, a group of periods of similar magnitude begins to emerge in the set of threshold periods when the probability of detection is increased. This phenomenon was employed to simplify the method.

4. Practical testing of the method demonstrated that the time taken to carry out an experiment is considerably shortened and the accuracy of its result is improved in certain threshold studies. /176

In conclusion, the author is indebted to S. G. Yurov for valuable remarks during discussion of the results and to V. P. Vasin and V. I. Skoblova for assistance in the experimental studies.

REFERENCES

1. Meshkov, V. V. Osnovy svetotekhniki (Principles of Light Engineering), Pt. 2. Gosenergoizdat, Moscow, 1961.
2. Blackwell, H. R. Journ. Opt. Soc. Amer., 36, 624, 1946.
3. Le Grand, Y. Light, Colour and Vision. Chapman and Hall, London, 1937.

All-Union Light Engineering Research Institute

COMPARISON OF THE BINOCULAR FUNCTIONS DURING ISO- AND ANISOMETROPIA

Yu. Z. Rozenblyum

The author finds that the depth of interruption of binocular vision depends primarily on the degree of anisometropia and on the depth of amblyopia of the poorer eye. Binocular vision is somewhat worse in hypermetropic refraction than in myopic and unlike refraction. The most informative test characterizing binocular vision in anisometropia is the determination of the relative depth of objects in stereopairs. Stereoscopic vision can occur even in the absence of binocular fusion in other tests (color test and diploscope).

Disruption of binocular vision, which has been sufficiently well studied in the case of strabismus, has hardly been studied at all in the case of anisometropia.

/177

At the same time, the difference in refraction of the two eyes may cause a considerable difference in absolute visual acuity [6, 3] and a corresponding impairment of the binocular functions should be anticipated.

In order to evaluate the impairment, the results of various tests characterizing the state of binocular vision during iso- and anisometropia were compared.

Examined were 67 people, aged 15 to 35 without visible * strabismus, with a difference in refraction of the two eyes of greater than 0.5 D in spherical equivalent or of greater than 1.0 D in degree of astigmatism. The control group was made up of 40 people in whom the difference in refraction of the two eyes did not exceed 0.5 D in spherical equivalent and 0.75 D in degree of astigmatism. The refraction of all the subjects was studied after triple application of 1% homatropine. Considered was a glass yielding the best vision, the astigmatism being determined by means of tests with a cross-cylinder and from the figure of a cross.

* Meant here by "visible" strabismus is only a distinct deviation of the eye as revealed by Hirschberg's method.

Binocular vision was studied with a PBI instrument (projector for binocular research) built by the All-Union Institute of Medical Instrument Construction. This is a projector built along the lines of a daylight movie projector. The test object was projected by slides onto a matte-finish screen measuring 20×20 cm from behind the test subject. The fields of vision of the two eyes were split up in all tests, except for Worth's dots, by placing polaroid films on the slides.

The following test objects were used.

1. A stereopair consisting of five pairs of geometric figures with transverse disparity ranging from 2' to 12' (Fig. 1). The response was evaluated by a five-point system: without errors — "5". With an error in estimating the position of a figure by one place, one point was subtracted. The numbers of such errors is greater than three, and also the inability to estimate depth or merging was evaluated as "1".

2. Diplograms, containing both alphabetical letters as well as figures (Figs. 2 and 3). The composite symbol one was in the form of the letter "B" (P and b, the vertical band common to both eyes); other symbols were in the form of a small mushroom and a diamond in two halves.

/178

3. The "four Worth's dots." (Fig. 4). In this case the fields were partitioned by red-green meshes.

All the tests were made from a distance of 5 meters in a darkened room. The use of the PBI device made it possible to carry out all the investigations under the same conditions. The tests were changed by turning the disk with the slides. The advantages of the device consisted not only in the rapidity of changing tests, but also in the prevention of the subject from knowing which figures to expect on the screen in advance.

In addition to these tests, the phoria of each test subject was changed on the Maddox cross (by the strength of the prism compensating deviation of the red line), and the presence of deviation of the eyes and of reverse adjusting motion was determined using a test with overlap.

Stereoscopic vision was studied not only with the PBI, but also with an ordinary lens stereoscope. Used as the test object were three small circles with a transverse disparity of 1 and 3°.

In hypertropic anisometropia (AM) the indices of binocular vision were somewhat poorer than in myopic and mixed AM. This is particularly clearly evident from the results of determining the relative depth from stereopairs projected with the PBI: in hypermetropia, 17 incorrect responses (i.e., more than half!), 10 inexact and 2 exact; in myopia, 9 incorrect, 4 inexact and 10 exact. The difference in reading the diplograms, and especially in reading the indications of the color test, was considerably less convincing.

A much greater discrepancy in the results of all the tests is obtained when the AM is grouped according to the difference in refraction, especially according to the degree of amblyopia. When the vision of the poorer eye is 0.3 and less (amblyopia of moderate and higher degree) [1], there was not a single instance of success in getting stereoscopy with the PBI instrument, and only three subjects determined the relative depth with studies using the lens stereoscope. This agrees generally with data demonstrating the absence of fusion when the vision of the poorer eye is lower than 0.3-0.4 [5]. To be noted is the appreciable divergence between the results of all three types of study of binocular vision. The color test yields the greatest number of correct responses in all forms of AM ($\sim 76\%$), the divided figures of the diplogram somewhat fewer ($\sim 73\%$), then the stereopairs ($\sim 63\%$) and, finally, the subjects fused the composite figure or letter on the diploscope the least successfully ($\sim 6\%$).

In isometropia the same tests yield respectively 100, 100, 77 and 4%.

It should be kept in mind, however, that not all the subjects possess the capability of fusing stereopairs. A certain amount of training is necessary to determine the relative depth. Moreover, with a slight displacement of the polaroids a second image may appear, inhibiting fused perception of a pair. When the PBI is used as a diploscope, the task of the subject is easier: merely name the visible objects. These considerations suggest that the percentage of correct answers in the stereoscope case is somewhat low.

Striking is the high capability of matching image pairs when, so it seems, it is difficult to anticipate the presence of stereoscopic vision. Some examples are given below.

1. Subject G. Right eye: sphere B 4.0 D and cylinder +1.0 D, 90° axis = 0.8; left eye: sphere + 6.0 D and cylinder + 1.0 D, 90° axis = 0.1. Vision is monocular on the diploscope. Stereopairs (on the lens stereoscope) match and determine the relative depth correctly.

2. Subject S. Right eye: sphere +1.0 D and cylinder +1.0 D, 70° axis = 1.0; left eye: sphere - 2.75 D = 1.0. Variable deviation of the right eye outward. Excellent stereoscopic vision with both instruments.

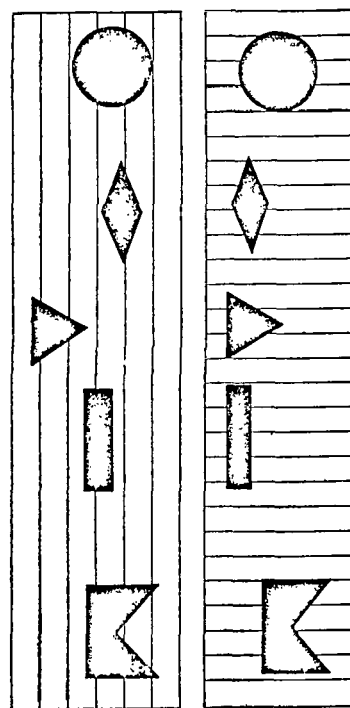


Figure 1. Stereopair. The Horizontal and Vertical Lines Indicate the Orientation of the Polaroid Films.

/179

/180

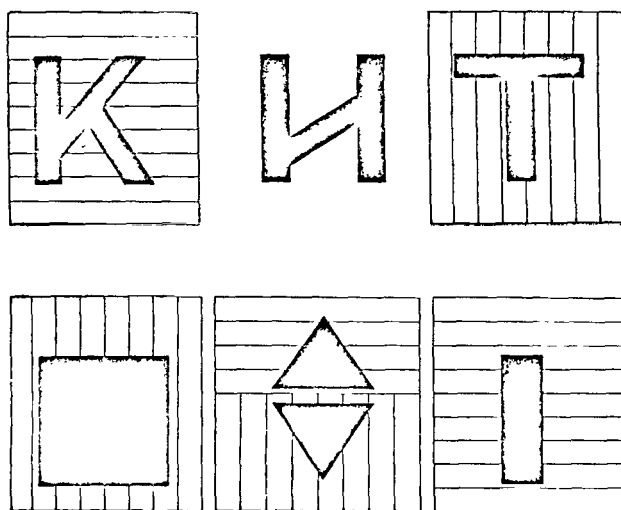


Figure 2. First Diplogram.

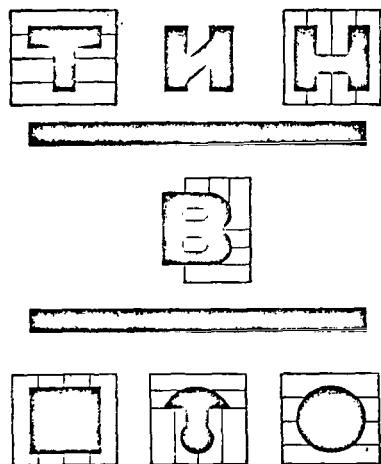


Figure 3. Second Diplogram.

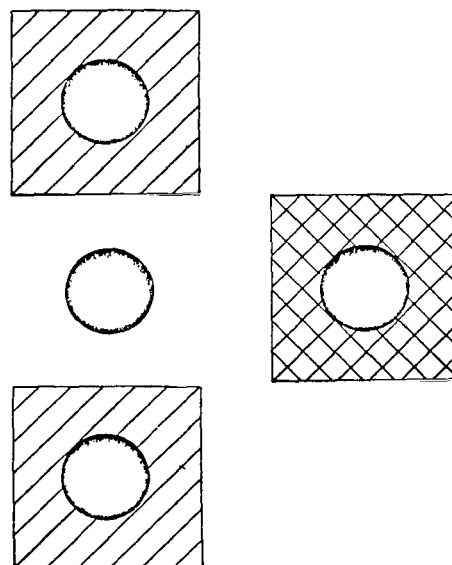


Figure 4. Four-dot Test. The Oblique Lines Indicate the Green Light Filter, the Mesh the Red Filter.

The high capacity of the visual system for stereoscopic vision is also indicated by the following fact: eight test subjects exhibiting incorrect binocular vision in the color test and with the diploscope (three in the color test, four with the diploscope, and two with the color test and the diploscope) were found to have stereoscopic vision, to the point of being excellent.

These data do not fit the usual idea of the "stage-like nature" of the development (and recovery in the case of pathology) of binocular vision: first appears simultaneous perception, then fusion and finally, as the highest function, stereoscopic vision [2, 4].

The presence of identical (or horizontally disparate) contours in the field of vision of the two eyes is apparently the most powerful stimulus for the matching of images.

CONCLUSIONS

1. The depth of interruption of binocular vision depends primarily on the degree of anisometropia and on the depth of amblyopia of the poorer eye.
2. Binocular vision is somewhat worse in hypermetropic refraction than in myopic and unlike refraction.
3. The most informative test characterizing binocular vision in anisometropia is the determination of the relative depth of objects in stereopairs.
4. Stereoscopic vision can occur even in the absence of binocular fusion in other tests (color test and diploscope).

REFERENCES

1. Avetisov, E.S. Uchebnyye zapiski instituta Gel'mgol'tsa (Scientific Notes of the Helmholtz Institute) 11, 1964.
2. Pil'man, N.I. Funktsional'noye lecheniye sodruzhestvennogo kosoglaziya u detey (Functional Treatment of Concomitant Strabismus in Children) p. 120, Kiev, 1959.
3. Rozenblyum, Yu.Z. Tezisy 5-go soveshchaniya po fiziologicheskoy optike (Abstracts of the Reports of the 5th Conf. on Physiological Optics) p. 122, 1966.
4. Sergiyevskiy, L.I. Sodruzhestvennoye kosoglaziye i geteroforii (Concomitant Strabismus and Heterophoria) 162, Moscow, 1951.
5. Smol'yaninova, I.L. Uchebnyye zapiski instituta Gel'mgol'tsa (Scientific Notes of the Helmholtz Institute) 11, p. 51, 1964.
6. Jampolsky, A., B.C. Flom, T.U. Weymouth and E.M. Lincoln. Arch. Ophthalmol., 54, No. 6, pp. 903-905, 1955.

Narofominsk

Translated for the National Aeronautics and Space Administration by
Scripta Technica, Inc. NASW-2036



023 001 C1 U 04 711119 S00903DS
DEPT OF THE AIR FORCE
AF WEAPONS LAB (AFSC)
TECH LIBRARY/WLOL/
ATTN: E LOU BOWMAN, CHIEF
KIRTLAND AFB NM 87117

POSTMASTER: If Undeliverable (Section 158
Postal Manual) Do Not Return

"The aeronautical and space activities of the United States shall be conducted so as to contribute . . . to the expansion of human knowledge of phenomena in the atmosphere and space. The Administration shall provide for the widest practicable and appropriate dissemination of information concerning its activities and the results thereof."

— NATIONAL AERONAUTICS AND SPACE ACT OF 1958

NASA SCIENTIFIC AND TECHNICAL PUBLICATIONS

TECHNICAL REPORTS: Scientific and technical information considered important, complete, and a lasting contribution to existing knowledge.

TECHNICAL NOTES: Information less broad in scope but nevertheless of importance as a contribution to existing knowledge.

TECHNICAL MEMORANDUMS: Information receiving limited distribution because of preliminary data, security classification, or other reasons.

CONTRACTOR REPORTS: Scientific and technical information generated under a NASA contract or grant and considered an important contribution to existing knowledge.

TECHNICAL TRANSLATIONS: Information published in a foreign language considered to merit NASA distribution in English.

SPECIAL PUBLICATIONS: Information derived from or of value to NASA activities. Publications include conference proceedings, monographs, data compilations, handbooks, sourcebooks, and special bibliographies.

TECHNOLOGY UTILIZATION PUBLICATIONS: Information on technology used by NASA that may be of particular interest in commercial and other non-aerospace applications. Publications include Tech Briefs, Technology Utilization Reports and Technology Surveys.

Details on the availability of these publications may be obtained from:

SCIENTIFIC AND TECHNICAL INFORMATION OFFICE

NATIONAL AERONAUTICS AND SPACE ADMINISTRATION
Washington, D.C. 20546